

National Park Service
Channel Islands National Park

**STATUS AND ECOLOGY OF DEER MICE (*Peromyscus maniculatus* subsp.)
ON
ANACAPA, SANTA BARBARA, AND SAN MIGUEL ISLANDS, CALIFORNIA:
SUMMARY OF MONITORING 1992 - 2000**

Technical Report 01-02

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August, 2001

Acknowledgements

Over the years of this study, numerous people collected data that are included in this report. Greg Austin, Susan Coppelli, Julie Goldzman, Patricia Hartman, Aaron Hebshi, Don Jones, Keith Rutz, and Andrea Lehotsky have each contributed many weeks and, in some cases, months to the mouse data collection effort. In the course of her Master's field work, Heidi David conducted extensive trapping on San Miguel Island that contributed greatly to the database. Paige Martin has collected mouse data on many occasions on Santa Barbara Island and assisted us with seabird data analysis. Kathryn McEachern and Dirk Rodriguez generously assisted with vegetation data analysis. Charles Drost, Gary Fellers, and Paul Collins graciously reviewed early drafts of the paper and provided many worthwhile suggestions. Gregg Howald and Holly Gellerman of the Island Conservation and Ecology Group shared data collected during the course of the Anacapa Restoration Project. Finally, thanks to Gary Davis and Bill Halvorson for their continuing efforts to promote the importance of long term ecological monitoring despite the constant realities and frustrations of actually getting it done.

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ABSTRACT

Monitoring of island deer mice (*Peromyscus maniculatus* subsp.) populations was conducted as part of the long-term ecological monitoring program at Channel Islands National Park from 1992 to 2000. Three subspecies of deer mice were monitored on nine grids on Anacapa, San Miguel, and Santa Barbara islands. Density and population numbers were estimated from mark/recapture data. Weight and sex information was also collected, and information on animal movement was obtained by analyzing trapping results. Density estimates among all islands ranged from less than 10 mice per hectare to over 900 per hectare. Fall densities were correlated with previous winter rainfall but not with any measure of vegetation. Spring densities were positively correlated with precipitation occurring during the winter two years previous, with spring vegetation measurements from the previous year, and negatively correlated with current-year winter rainfall. Average adult weights were consistently higher on Santa Barbara during all periods studied. Weights on Santa Barbara and San Miguel islands were significantly different among habitats, being higher in shrub habitat than in grasslands. There were few relationships between density and measurements of dispersal, although on San Miguel Island there was a significant positive relationship between the number of single captures and density. Spring densities of mice on Santa Barbara Island were compared with the amount of predation on Xantu's murrelets (*Synthliboramphus hypoleucus*) during the spring nesting season and no relationship was found. Mouse predation was found to negatively affect annual productivity of murrelets. Mice were found to have a significant negative relationship on short-term *Coreopsis* productivity on Santa Barbara Island. On San Miguel Island mouse densities rose sharply after a population crash of island foxes (*Urocyon littoralis littoralis*) resulted in the elimination of the fox as the primary predator from the system. Population numbers apparently cycled with a three to four year periodicity on Santa Barbara Island, however no cyclic patterns were apparent on Anacapa or San Miguel islands. Density tolerance appears to be extreme on Santa Barbara Island and a result of adaptation, while on San Miguel Island indications are that predation functioned to limit population numbers and tolerance for high densities is reduced. Finally, suggestions are provided for application of mouse monitoring data in selecting alternatives for two current management issues.

INTRODUCTION

Deer mouse populations have been monitored with mark-recapture techniques as part of the terrestrial vertebrate monitoring program at Channel Islands National Park since 1992. The monitoring protocol (Fellers et al. 1988) for deer mice was designed to identify changes in population status, and to evaluate the general health of the populations utilizing weight, age, sex, and reproductive information. Annual data from the program were presented in Schwemm 1995, Schwemm 1996, Austin 1996, and Austin 1998.

Aside from these reports there are few recent studies of small mammals from any of the eight California Channel Islands. Two notable exceptions are 1) a resource study completed for the National Park Service (Powers 1979) which includes a very detailed description of island deer mouse ecology and the results of a one-year study of population numbers on Santa

Barbara Island by Collins, Storrer and Rindlaub, and 2) a follow-up study (Drost 1989, Drost and Fellers, 1991) which examined an eight-year period of mouse population cycles on Santa Barbara Island and presented conclusions regarding the likely effects of predation and weather factors on mouse numbers. Two studies have been prepared which discuss harvest mice (*Reithrodontomys megalotis*) on the islands, (Collins 1987, Perlmutter 1993), Collins and Martin (1985) summarized information regarding the Santa Catalina Island shrew (*Sorex ornatus willetii*), several papers have been written regarding genetic studies of Channel Islands populations of *Peromyscus* (Gill 1980, Pergams and Ashley 1999, Pergams and Ashley 2000), and one recent paper reported on a one-year deer mouse population study on Santa Cruz Island (Mayfield et al. 2000).

As part of the vertebrate monitoring program, deer mice have been sampled on three islands within the park since 1992. A total of 92 trapping sessions have resulted in the capture of approximately 7,300 individuals. In

this report we summarize the weight data, dispersal information, and population and density estimates from this sampling, and examine these results for four purposes:

1. To evaluate the overall health and trends of the mouse populations on the islands. The purpose of the vertebrate monitoring program is to regularly measure several population and individual indices to gauge the status of populations over time. In this paper we examine all the data from the last nine years, both by individual island and parkwide, in an attempt to detect long-term trends in population dynamics that may not be obvious from annual data summaries.
2. To investigate possible relationships between changes in mouse numbers and changes in other components of island systems. With the exception of a localized population of harvest mice (*Reithrodontomys megalotis*) on Santa Cruz Island, deer mice are the only member of the native small mammal community on these islands, a trophic level that includes many taxa on the adjacent mainland. For this reason, and because mice are so numerous, their role as both prey and predator is significant. Here we examine monitoring data from other park monitoring programs which describe island fox populations, seabird populations, and vegetation communities to look for changes over time in those groups which may affect or be influenced by changing mouse densities.
3. To add these data to the body of work which focuses on small population dynamics within island habitats. These data were not collected as part of a research effort; however they may be of interest in the study of island biogeography. We have population and density estimates from several habitat types on three islands for nine years, and we present these in the context of several theories regarding organization and functioning of rodent populations on islands.
4. To provide information regarding deer mouse ecology for management decision-making within the park. Two specific issues are discussed which directly affect or are affected by the status and ecology of deer mice on Santa Barbara and Anacapa

islands, and summary data such as these will hopefully aid in the successful recovery of island natural systems.

Population health and trends

The primary purpose of the monitoring program at Channel Islands National Park is to know enough about the resources over which we have management authority to assess the condition of the resource at any given time and be prepared to take action should the resource appear to be threatened or unhealthy. It is probably safe to say that at the present time there are no significant threats to the persistence of deer mice on the islands. Deer mice are extremely numerous, are not habitat-specific, and are not susceptible to any pollutants or diseases that we know of. Total predation on mice by all natural predators on the islands is minimal compared to that occurring in most mainland systems. And while Hanta virus and general health concerns do necessitate that mice be removed from human-occupied buildings, currently the number of mice eliminated from the population by humans on any given island is insignificant to the stability of the population as a whole.

We should not, however, assume that the island mouse populations will never be threatened or could never be eliminated, especially on the smaller islands of Anacapa and Santa Barbara. Several endemic rodents are presumed extinct from islands off the West Coast of Baja California in Mexico, including *Peromyscus maniculatus cineritius* (Alvarez-Castaneda and Cortes-Calva 1996). While park islands are better protected than some of the Mexican islands, the impacts of non-native animals could be as great here. The possibility of some medium-sized animal such as a cat reaching the islands is unlikely but not impossible. Should a pregnant cat be introduced to an island and not quickly removed the results could be severe. The introduction of house mice (*Mus musculus*) is more likely and could go undetected for many years. The possibility of such an introduction and the effects such an event would have on native mice must be taken seriously.

As will be discussed below, mice were absent from East Anacapa Island for approximately 20 years. What caused the loss of

mice from that island is not known. We must assume that the same event or series of events could happen again on Anacapa or on other islands. Finally, efforts to eliminate black rats from Anacapa and San Miguel islands will have temporary but negative effects on mouse populations. For these reasons it is important that the park continue to monitor deer mice and present monitoring data for review to NPS and outside biologists.

Deer mice in island communities

Twelve monitoring protocols are currently in place for the biological and physical resources within the park, but few attempts have been made to integrate the results from these separate efforts. While these programs allow us to increase our knowledge of selected species and groups, we have a long way to go before we will understand and can manage island ecosystems as the primary functional units of importance. Because mice are present on every island and interact in some manner with all other resources, a greater knowledge of the role of mice within the system would be useful in this effort. In this report we examine the data from several monitoring programs as they may reflect the relationships between mice and vegetation communities, mice and seabirds, and mice and island foxes.

Park vegetation has been monitored since 1984. Point-intercept data are recorded along permanent transects to monitor changes in species composition in representative island habitats (Halvorson et al. 1988a). The vegetation monitoring transects for Santa Barbara, Anacapa, and San Miguel islands were first established in 1984, and data have been collected mostly annually since then (Johnson 1998). However the relationships, if any, between vertebrate population dynamics and changes in land cover on the islands have not been previously addressed. In this report we compare measurements of vegetation composition with mouse population data in areas where mouse grids correspond with vegetation transects.

Because they occur in such great numbers, it has been proposed by some that deer mice may at times have negative effects on some species. For example, it has been suggested that at very high densities mice may significantly reduce the reproductive success of

Xantu's murrelets (*Synthliboramphus hypoleuca*) on Santa Barbara and Anacapa Islands (Murray et al. 1983, Sydeman et al. 1996, McChesney et al. 2000). Mice prey on murrelet eggs and nestlings, and are often observed in the murrelet breeding colonies during the springtime nesting period (P. Martin pers. comm.). Data on the number of predated eggs are collected annually as part of the seabird monitoring program on Santa Barbara Island, however the amount of observed predation has never been compared to measurements of mouse numbers. In this report we assess the level of correlation between annual springtime densities of mice and the percentage of murrelet eggs predated by mice on Santa Barbara Island.

Impacts by deer mice are also suspected of retarding recovery of giant *Coreopsis* following removal of rabbits from Santa Barbara Island. Salas (1990) hypothesized that an absence of young *Coreopsis* plants in the canyons might be due to seedling herbivory and seed predation by mice. It is also probable that mice have similar impacts on other plant species, however there has been no directed analysis of vegetation and mouse monitoring data to evaluate this suggestion. Here we look at the relationship between mice and *Coreopsis* to begin to understand the role of mice as seed and plant predators.

Of the three islands in this study only San Miguel is large enough to support the endemic island fox (*Urocyon littoralis*). The presence of the fox as a predator of mice on this island distinguishes the community from those on Santa Barbara and Anacapa islands where foxes are absent. Within the San Miguel system the mice have evolved with the fox as a predator, while on the other islands they have not. Unfortunately the fox population on San Miguel is currently threatened with extinction. Only 17 adult foxes remain on the island, (from a population of over 400), and all but one are in a captive breeding facility. It is sadly ironic that the loss of this animal from the system is providing biologists with a unique opportunity to study the San Miguel system as it responds the removal of the fox. The long-term impacts to the system may be profound, since foxes will probably not be released back to the wild in significant numbers for many years. For this report we compare monitoring data for the mouse and fox populations during the period of fox decline and ultimate removal.

Finally, we examine mouse densities as they may relate to changes in seasonal rainfall. It is theorized that higher amounts of rainfall positively affect mice by increasing seed production and amount of cover, but also that a severe amount of precipitation during the winter may increase winter mortality of mice. We look at both winter rainfall of the current year and rainfall of the previous winter season as it relates to estimated mouse densities during spring and fall seasons.

Island biogeography and rodent population dynamics

Finally, we examine the population dynamics of the Channel Islands mice as they relate to current theories regarding small mammal population dynamics within island habitats. In the last several decades it has been recognized by many authors that an understanding of processes on natural islands will improve our chances of preserving resources in the increasing number of habitat patches created by human development (Wilcove et al. 1986; Burkey 1995; Newmark 1995). Consequently, a large body of work has focused on the differences between population regulating mechanisms of animals in open, contiguous habitats and those on islands and within habitat patches. Studies looking specifically at demographic parameters of small mammal communities have concluded that insular populations of rodents are generally characterized by increased densities, decreased vagility and reduced dispersal (Sullivan 1977; Tamarin 1978; Gliwicz 1980; Crowell 1983; Krohne and Hoch 1999). In this paper we utilize data obtained from the monitoring program to assess the level to which the mouse populations on the Channel Islands demonstrate these characteristics.

Dispersal

For this discussion we define dispersal as the permanent departure of an animal from its home range. This activity may or may not result in the successful establishment of the animal in a new home range. The purpose and adaptive significance of dispersal have been extensively studied, particularly in rodents (Stickel 1968; Gadgil 1971; Lidicker 1975; Gaines and McClenaghan 1980; Anderson 1989). According to these authors, dispersal is an important demographic parameter which influences the regulation of numbers and productivity, and is one

of the most important factors of population biology.

In its most common manifestation, dispersal will occur when an individual perceives its physical and social environment to be disadvantageous (Anderson 1989). Most often this occurs to animals which are less fit and results in the emigration of these individuals. Many theories have been proposed to explain the mechanisms which cause dispersal in rodents (Lidicker 1975; Gaines and McClenaghan 1980), however there seem to be three general categories of dispersers: 1) young animals dispersing from their natal range; 2) adults leaving unsaturated habitat; and 3) adults leaving saturated habitat. For this discussion we attempt to relate an index of dispersal activity within the population to the state of the population regarding relative density and cyclic activity.

To study dispersal one must distinguish between individuals who are actually leaving the home range and those who may be simply foraging or investigating potential new habitat areas. Such individuals could not be identified from our data, so instead we looked at two indirect measures of dispersal. First, we examined the mean maximum distance moved, or MMDM, as calculated for each individual by CAPTURE. (The MMDM is estimated by determining all the traps at which a particular individual is captured and then averaging the distance the animal must travel to reach those traps.) Second, we looked at the number of animals captured only once during a trapping event. For this analysis we used all age classes to include dispersing young. Animals captured several times during a trapping session can be considered to be resident, while animals captured only once are more likely to be transients. Similar techniques have been used in previous studies to suggest identities of animals exhibiting various travel behaviors (Gaines and McClenaghan, Jr. 1980 for review, Extine and Stout 1987, Ribble 1992, Wolff et al. 1996). We present this relative index of residents versus transients in a population to suggest the level of dispersal occurring at any given time. Additionally we examined the average weights of transients compared to residents for a suggestion of the relative fitness of each group.

Many studies have shown that dispersal of all types is less common in rodent populations on islands than it is in open populations (Crowell 1983, Redfield 1976, Sullivan 1977). It has been

generally theorized that reduced dispersal tendencies on islands are an adaptation to the fact that on an island the risks associated with dispersal are greater than the potential benefits (Redfield 1976, Tamarin 1977, Gliwicz 1980). Dispersing individuals are more susceptible to predation and other dangers, and in general suffer higher rates of mortality than do non-dispersers. Consequently a population without significant dispersal tendencies will generally fluctuate less than will a population with many dispersing individuals, since fewer animals are lost to dispersal-related mortality (Tamarin 1977). In contiguous habitats the potential benefits of dispersal, such as establishing a home range in a better habitat, the location of potential mates, and removal from genetically related conspecifics, may be great enough that overall the success of the species will increase. On true islands, however, there may in reality be nowhere to disperse to, and therefore there are few benefits to the behavior to outweigh the risks.

Sullivan (1977) also observed less aggression in island mice than in mainland individuals, and has proposed that behavioral differences might account for lower amounts of dispersal. If aggression is reduced, then dispersal will be less, and animals might in general be more tolerant of each other and experience less mortality as a result of aggressive interactions.

Island biogeographic theory explains that the size of an island on which a species evolves is significant to the evolutionary trend of that species (MacArthur and Wilson 1967). It remains unclear at what point the size of an island becomes so great that it ceases to impart those pressures that act to direct adaptation toward island-oriented speciation. It is quite possible that in the case of the California Channel Islands the smaller islands have functioned to alter the ecology of deer mice while the larger ones have not. For this study we are assuming that the islands are small enough that *Peromyscus* speciation resulting in unique behaviors and ecology likely occurred to some degree, but that suggestion remains open to investigation.

Density

Small mammal populations on islands consistently exhibit higher densities than do similar populations in mainland habitats (Gliwicz 1980 for summary; Crowell 1983; Krohne and Hoch 1999). Drost and Fellers (1991) found this

to be especially true on Santa Barbara Island, where densities for *P. maniculatus* were higher than any previously recorded in the literature. The presence of so many individuals of a single species functioning as predators of seeds and eggs as well as prey for carnivores and raptors has implications for other ecosystem elements. The sheer biomass that these numbers represent is impressive; using Drost and Fellers' high estimate of 462 mice/ha and an average weight of 20g/mouse results in a potential estimate of 2,384 kg, or 5,269 pounds of mice on 1mi² Santa Barbara Island during that period, assuming some habitats support more and some fewer numbers of animals than that sampled in their study.

It has been suggested that island systems may promote within a species a tolerance of increased density to protect against extinction (Tamarin 1978; Gliwicz 1980). In contiguous habitats or areas of metapopulations, the loss of one localized population will not result in the permanent loss of genetic information. If metapopulation dynamics are functioning then genetic makeup will be maintained overall. In island environments, however, a crash or extinction would be fatal for a population, since no adjacent populations exist from which to recruit replacement individuals. To prevent such an extinction the population must consistently maintain higher numbers.

In addition to being advantageous, maintenance of high densities may also reflect the release of competitive and predatory pressures on islands (Crowell 1983; Drost and Fellers 1991). Research on islands with and without predators has described higher densities on islands where predators were absent (Crowell 1983). In this report we compare densities in similar habitats on Santa Barbara and Anacapa islands that have never supported island foxes, with San Miguel Island that has until recently supported fox populations. (There are currently no wild island foxes on the islands in this study, however we do have data from several years when foxes were abundant). Similarly, competition for space and resources from other small mammal species would work to limit the number of any one species. *Peromyscus* is rarely the only member of the small mammal assemblage in a habitat, as it is on these islands. In most mainland environments *Peromyscus* species share habitat with one to several other *Peromyscus* and often with many other rodents (Kaufman and Kaufman 1989,

Schwemm 1993). When populations are limited less by interspecific competition and predation, densities may increase to carrying capacities determined primarily by other factors such as habitat availability and quality, food supply, and intraspecific competition.

Population cycles

The occurrence of population cycles has been studied in many small mammal groups (Myers and Krebs 1974 for summary; Krebs and Wingate 1985) and in deer mice in particular (Jameson 1955). Several theories have been proposed to explain the causes of these cycles, including internal regulation and external factors. Generally, such observations of large variations in population numbers of small mammals have been absent from island systems. Several studies have suggested that island populations of rodents generally display greater stability of numbers over time than do other systems (Gliwicz 1980 for review). However, Drost and Fellers (1991) reported that the deer mouse population on Santa Barbara Island fluctuated every three to four years, and displayed cyclic tendencies more similar to populations found in mainland contiguous habitats than to any previously studied deer mouse population. If so, the population dynamics on Santa Barbara Island are consistent with island theory in the case of the high numbers of animals, but are inconsistent because the numbers vary greatly from year to year.

According to population regulation theory, then, either dispersal on Santa Barbara Island is more common than reported for other island populations and dispersal-related mortality contributes to population fluctuations, or dispersal is still reduced, and some other factor or factors drives the changes in populations numbers. This second theory was suggested by Drost and Fellers (1991) who identified predation as a significant external force that affects mouse populations.

In this paper we compare the density data obtained from Santa Barbara Island from our monitoring to the Drost and Fellers study to examine whether or not their observed trends have continued. We also examine data from Anacapa and San Miguel islands for cyclic patterns that may or may not be synchronous with those on Santa Barbara Island. We also compare

population estimates from grassland habitat across islands in the same years. Finally, we investigate the relationship between density and average adult male weight to determine whether or not individual fitness changes in response to long-term population fluctuations.

Importance of vertebrate monitoring

Small mammals, commonly species of *Peromyscus*, are present in some numbers in almost every terrestrial ecosystem. Deer mice in particular may be the most widely-distributed native small mammal on the continent (Hopper 1968). Small mammal research has focused on numerous aspects of ecology and biology, however these studies have often been conducted under laboratory conditions, or in systems where two or more species coexist. Consequently, the presence of several native populations of deer mice existing in closed but natural conditions, and as a single member of the small mammal community, as is the case on the Channel Islands, encourages many comparisons to deer mice as they function in less isolated situations and as members of a more diverse rodent community.

Deer mice on the islands are of ecological and management interest for several reasons. In addition to the impacts of mice on murrelets, it is also suggested that at high densities deer mice may prey heavily on the native giant *Coreopsis* (*Coreopsis gigantea*), girdling and damaging many plants (K. McEachern pers. comm.) Efforts to remove non-native rats (*Rattus rattus*) from Anacapa and San Miguel islands will likely have temporary but significant impacts on the mouse populations on those islands. Deer mice are the only native small mammal on these islands, making their role as seed dispersers potentially extremely important (Boyd 1991). In coming years the response of the mouse population on San Miguel Island to the removal of the island fox will be dramatic and will likely result in minor as well as possibly significant alterations to the system as a whole. Finally, deer mice on the Channel Islands function as a vector of Hanta virus, and this situation is of concern, particularly in areas of high visitor activity.

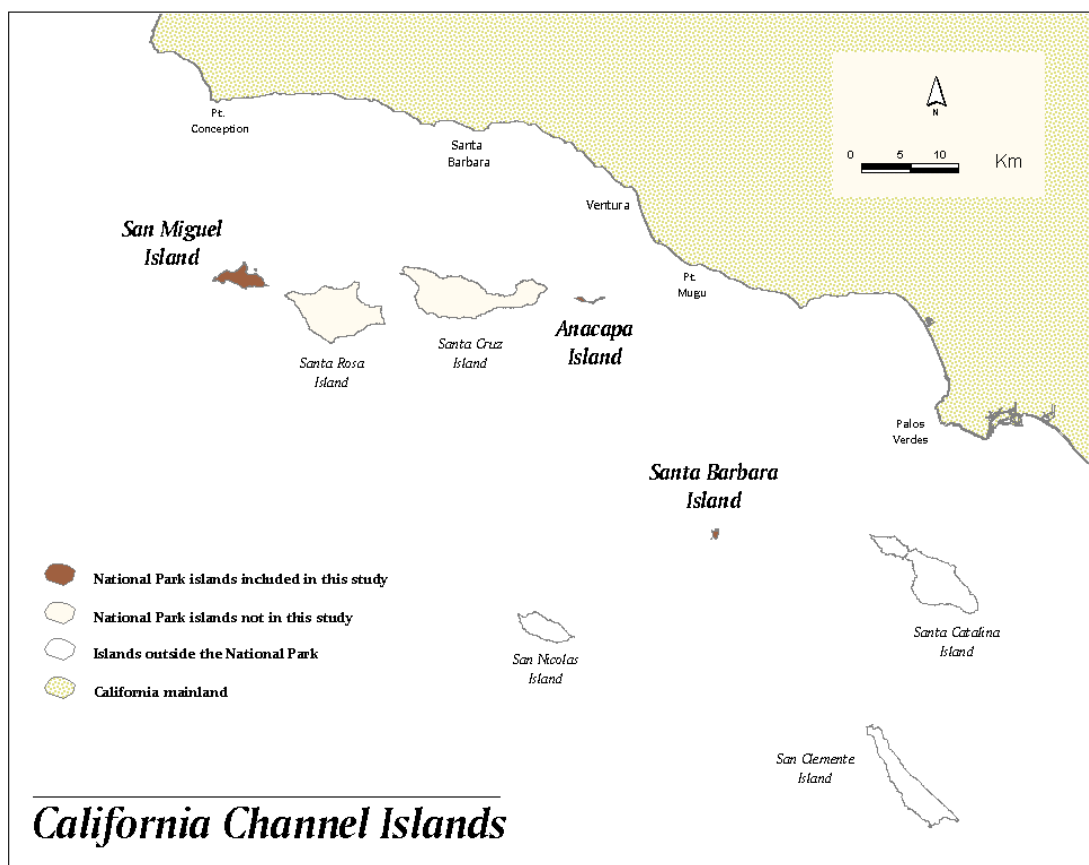


Figure 1. Channel Islands National Park, California.

Study Area

Physical characteristics

The five islands that comprise Channel Islands National Park lie in a mostly east-west orientation south of Santa Barbara, and west of Los Angeles, California (Figure 1). These five islands are part of a larger group of eight islands collectively known as the California Channel Islands. Of the five islands within the Park, the National Park Service (NPS) owns three, Santa Barbara, Anacapa, and Santa Rosa, and co-owns Santa Cruz Island with The Nature Conservancy. San Miguel Island is owned by the US Navy and managed by NPS. The islands range in size from about 258 hectares (Santa Barbara Island) to approximately 25,000 hectares (Santa Cruz Island), and lie between

20 and 60 km from the California mainland coast.

Approximately 18,000 years ago the four northern islands of San Miguel, Santa Rosa, Santa Cruz, and Anacapa were connected as one land mass known as Santarosae. During the peak of the glacial period this mega-island measured approximately 188,000 hectares and was separated from the mainland by only five kilometers of channel. This landmass was never connected to the mainland, or to Santa Barbara, San Nicolas, San Clemente, or Santa Catalina islands to the south. The two sets of islands are usually referred to as the northern and the southern islands, respectively.

Deer mouse monitoring is currently conducted on San Miguel and Anacapa islands from the northern group, and Santa Barbara

Island from the southern group. The remainder of this report discusses only those islands.

The climate on the islands is predominately influenced by the Mediterranean weather pattern characteristic of Southern California. Summers are typically hot and dry, lasting from approximately June through November, while winters are cool and rainy, with most of the rain occurring between December and March. Hot, dry winds called Santa Anas often occur in the fall, when wildfires are most likely to occur. Island areas experience many weeks of foggy conditions during the spring and early summer, and fog may contribute significantly to the amount of fresh water available to plants and animals. The surrounding cooler ocean moderates the climate on the islands, and temperatures are generally not as extreme as on the mainland. Average summer high temperatures range from 66°F on westernmost San Miguel Island to 90°F at the interior locations on Santa Cruz and Santa Rosa islands. Average winter lows range from 30°F at interior locations to 51° on the smaller islands closer to shore. Days of frost or very high temperatures are rare (Channel Islands National Park data). Weather systems moving eastward across the Pacific result in many days of moderately strong northwesterly winds on the islands. Conversely, in the fall, when Santa Ana winds blow from the northeast off the deserts and across much of Southern California, the winds off the ocean negate these easterly winds and the islands often experience some of the calmest days of the year.

Natural environment

Like many islands the California Channel Islands are depauperate compared to mainland areas, and support relatively few terrestrial vertebrate species. Excluding bats, a total of only two mammal species, deer mice and island foxes, and five herptiles are native to these three islands. Several vertebrate and plant taxa have evolved as distinct insular species and subspecies as a result of geographic isolation from the mainland and from each other.

However, as is also true of many oceanic islands around the world, the introduction of non-native species has greatly impacted the native systems. Beginning in the mid-1880's humans began to bring to the islands

all manner of alien fauna; rabbits, cats, burros, sheep and rats were all present at one time on one or more of the islands. Along with the animals came crops and forage made up of alien plants, resulting in a significant conversion of the islands from native vegetation types to plant communities comprised predominantly of non-native grasses and herbs. The effects of grazing and trampling accelerated erosional processes and left many areas devoid of vegetation. Within the last 20 years most of the exotic animals have been removed; black rats are currently the only non-native animal still present on the islands in this study and are found on Anacapa and San Miguel islands.

Each island supports a unique subspecies of *Peromyscus maniculatus* and distinct morphological differences seen among the island populations suggest that very little gene flow currently takes place between islands. All of the present-day subspecies of *P. maniculatus* on the islands are larger than the subspecies on the mainland of Southern California *P. m. gambelii*. (Gill 1980). Mice on the four northern islands are more closely related to each other than to the subspecies from the southern islands, but all island subspecies are more closely related to each other than to mainland subspecies (Gill 1980).

Black rats (Rattus rattus)

The population status of black rats on the islands is currently unclear. Rats have been present on Anacapa since at least the early 1900's and have been noted by most of the inhabitants of the island since that time (Collins et al. 1979). Rats were not documented on San Miguel Island until 1970, but it is likely that they arrived much earlier (Erickson and Halvorson 1990). Rats most likely were introduced to the islands during shipwrecks, when rat-filled wooden boats were common and often crashed on the offshore rocks, and/or by human activities which brought building and construction supplies to the islands (Collins et al. 1979). Rats occupy most of the habitats on Anacapa, but apparently prefer the rocky cliffs which surround much of the island (Collins et al. 1979). Current work suggests that they may spend much of their time foraging in the tidepools at the base of these cliffs where they feed on marine invertebrates (G. Howald pers. comm.) On San Miguel Island it appears that until recently the rats were confined to the beaches on the northwest part of the island where they may

have originally arrived in one or more shipwrecks (Collins et al. 1979). However recent observations indicate that rats may slowly be expanding their distribution from the beaches up on to the terraces. Burrows that most likely were created by rats have been discovered in Native American (Chumash) middens (D. Morris pers. comm.).

The extent of mouse predation by rats and the degree of competition between the species are unknown. Collins et al. (1979) suggested that interspecific competition between rats and mice was responsible for the almost total elimination of mice from East Anacapa noted by them during the 1970's. Mice apparently were absent from the islet for about 20 years but returned to the islet sometime prior to 1996. The precise timing of the recolonization is unknown, nor is it known why mice returned after being absent for so long when rats are still present. The role of dispersal and the manner in which mice may have returned to East Anacapa will be discussed below. Efforts currently underway to remove rats from Anacapa include frequent monitoring of mice and rats, and in the next few years will provide significant information regarding the relationships between the two species.

Vegetation

The pre-European vegetation structure on the islands was probably a combination of Mediterranean-type chaparral and coastal dune and beach vegetation (Hochberg et al. 1979). Based on the discovery of what may be the earliest human remains found in North America to date, humans occupied the islands as early as 13,000 BP (D. Morris pers. comm.). Chumash people occupied the islands until about 1815, and likely altered the land cover make-up of the islands with the use of fire as a management tool (D. Morris pers. comm.). Ranching on the islands began in the mid nineteenth century with the arrival of European and Russian adventurers and their stock and continued until very recently. Grapes, hay, non-native grasses, and other crops were planted, and numerous alien plant species arrived on the islands as a consequence of ranching activities.

The removal of animals whose activities were particularly damaging to plants, such as rabbits and sheep, is resulting in a slow but measurable recovery within the vegetation communities. A combination of active restoration and natural succession will hopefully work to

overcome previous impacts. Because unique features and processes characterize each of the islands, individual descriptions are presented.

Santa Barbara Island

Santa Barbara Island (Figure 2) is the furthest south and east of the study islands. The forces of the warmer California counter-current dominate the processes around the southern islands so that the weather patterns here are markedly different from the islands to the north. Santa Barbara Island has less fog, fewer days of wind and warmer temperatures than either



Figure 2. Deer mouse monitoring sites on Santa Barbara Island, Channel Islands National Park, California.

Anacapa or San Miguel (Channel Islands National Park weather data).

The island is predominantly a marine terrace, with steep cliffs and few beaches making up the shoreline. Two peaks of moderate height are oriented north to south and dominate the main terrace of the island. These peaks and a resulting saddle rise above moderate slopes and gentle topography. To the west of this ridge is a sloping terrace that

descends to the ocean more gradually than do other areas of the island. To the east are several small canyons that run from east of the terrace to the ocean. The only human structures on the island are a landing dock, two buildings for housing personnel and equipment, and a water storage tank. Adjacent to the buildings is a campground. Collectively this whole developed area accounts for about 0.1% of the island.

The introduction of non-native species has been particularly devastating to the fauna and flora of this relatively small island. The first report of humans on Santa Barbara dates from about 1846, by which time goats were already present. Little is known about the vegetation structure before that time, although it is likely that much of the island supported large areas of giant *Coreopsis* and native bunchgrasses interspersed with patches of shrubs and cactus (Hochberg et al. 1979). Sheep were brought to the island prior to 1897, and by the 1920's much of the land had been cleared and burned for farming and ranching. *Mesembryanthemum crystallinum*, a fast-spreading introduced iceplant, was first reported from Santa Barbara Island in the late 1800's, and from that time expanded its distribution to the point where in the 1930's it was reported as being the major vegetation type over most of the island (Philbrick 1972).

A particularly destructive species of rabbit, *Oryctolagus cuniculus*, was introduced to the island in the 1920's and again in the 1940's. By the 1950's many *Coreopsis* stands were destroyed and all of the shrub communities were impacted to some degree by the grazing activities of this animal (Woodhouse 1979, Hochberg et al. 1979). A fire in 1959 destroyed most of the remaining stands of *Coreopsis* and shrubs on the eastern part of the island, which had also served as the primary nesting habitat for the endemic Santa Barbara Island song sparrow, (*Melospiza melodia graminea*). This bird was last seen in 1967 and is now presumed extinct.

All non-native animals have now been removed from Santa Barbara Island. However, recovery of the island's vegetation communities has been slow (Halvorson et al. 1988b, D'Antonio et al. 1992). Alien grasslands are the most common vegetation community on the island, replacing what were probably shrublands (Clark and Halvorson 1990), and alien taxa

make up 60% of the total vegetation cover on the island (Halvorson et al. 1988b).

The only native terrestrial vertebrate on Santa Barbara other than the deer mouse is the island night lizard (*Xantusia riversiana*). These lizards are Federally listed as endangered, but have been increasing in number with the recovery of the shrub/cactus habitat on which they depend (Schwemm 1995, Austin, 1998, C. Drost pers. comm.). Many seabirds nest on the island and offshore rocks, including brown pelicans (*Pelecanus occidentalis californicus*), Xantu's murrelets (*Synthliboramphus hypoleuca*), western gulls (*Larus occidentalis*), and several species of cormorants (*Phalacrocorax* spp.). During the nesting season pelican and gull nests can cumulatively cover many acres of land (P. Martin, pers. comm., NPS aerial photo data). Landbirds which prey on mice include barn owls (*Tyto alba*), short-eared owls (*Asio flammeus*), northern harriers (*Circus cyaneus*), and American kestrels (*Falco peregrinus*) (Jones et al. 1989, Coonan 1996).

Anacapa Island

Anacapa is the closest island to the mainland, lying approximately 15 kilometers off the coast of Oxnard, California (Figure 3). The greater island of Anacapa consists of three islets, East, Middle and West, which range in size from 47 hectares (East Islet) to 183 hectares (West Islet). The islets of East and Middle Anacapa are separated by less than 150 meters during average tides, and West and Middle Anacapa are at times closer than ten meters. East and Middle Anacapa are similar in topography, being mostly level terraces in the center of the island with steep, volcanic cliffs around much of the shoreline. West Anacapa is more diverse in its topography, having a mid-island ridge that runs east to west. Midway along this ridge is a peak which slopes gradually north into short, steep canyons. South of the ridge are steeper cliffs more similar to East and Middle Anacapa. There are no human-made facilities on West or Middle Anacapa and public access is restricted due to the presence during much of the year of nesting brown pelicans. Conversely, East Anacapa is the most-often visited island in the park, and four buildings and a lighthouse are clustered on the terrace near the east end of the island. The weather on Anacapa is similar to that of the mainland coast; days of fog and wind are common, and temperatures range from the mid

40's to the mid 70's. Average rainfall is about 38 cm/year.

were planted around the buildings. As forage for sheep became scarce, ranchers introduced

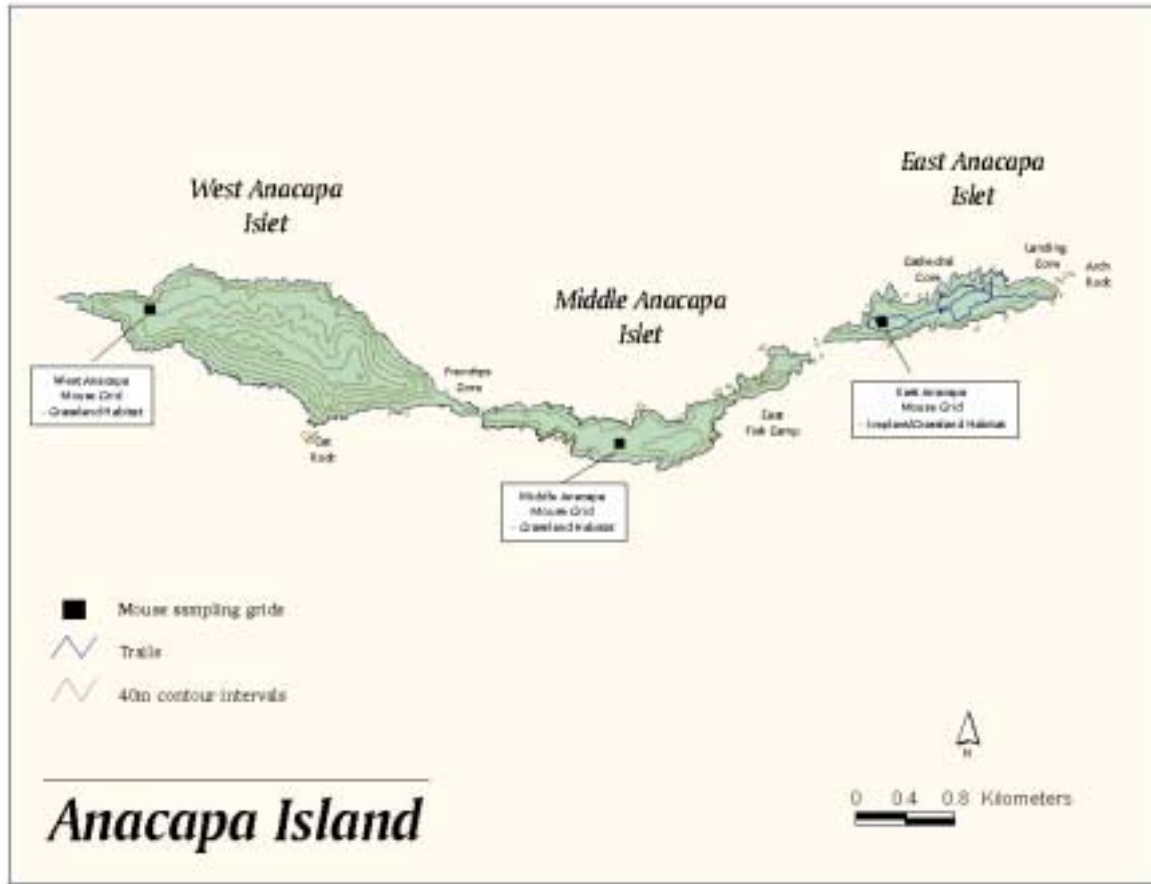


Figure 3. Deer mouse monitoring sites on Anacapa Island, Channel Islands National Park, California.

Greater topography on Anacapa results in a more diverse assemblage of plant communities than occurs on Santa Barbara or San Miguel islands. Vegetation on the island prior to human arrival was likely characterized by *Coreopsis* stands, native bunchgrasses, and native shrubs, similar to the current appearance of West and Middle Anacapa islands but without the non-native species (Hochberg et al. 1979). The first record of grazing is from 1902, but there may have been grazing during the 1800's, as evidenced by human activity on Middle Anacapa in 1853. Sheep were raised on East Anacapa between 1902 and 1937, and sheep may have persisted until as late as the 1960's. In 1928 a lighthouse and associated housing complex were constructed, and introduced plants, particularly iceplant (*Malephora crocea*)

annual species such as *Bromus* and *Hordeum*, which have become the dominant species in the grasslands on the island.

In addition to grasslands, *Coreopsis* stands and coastal bluff communities, West Anacapa Island also hosts areas of island chaparral and island woodland, which are not present on any of the other islands in this study. The north facing cliffs are mostly comprised of the sea cliff phase of coastal bluff scrub, or are almost continuous areas of *Coreopsis* (Hochberg et al. 1979). Other areas are characterized by the abundance of introduced iceplant almost to the exclusion of other species. Coastal sage scrub exists on south-facing slopes. The grasslands on Anacapa Island are richer in native perennial bunchgrasses than the grasslands of Santa Barbara Island, often

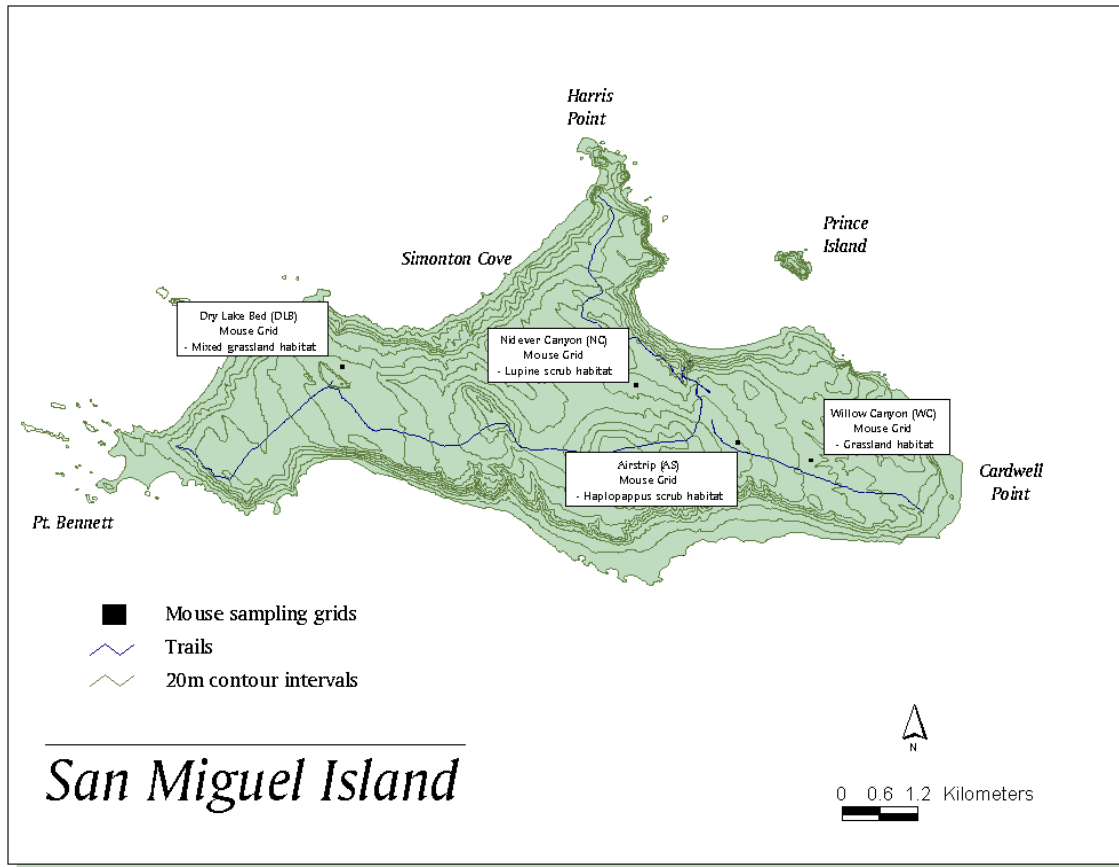


Figure 4. Deer mouse monitoring sites on San Miguel Island, Channel Islands National Park, California.

containing *Coreopsis*, *Dudleya*, and other native species. The three islets support the same subspecies of deer mouse, but genetic analysis shows that there are some minor differences (Pergams and Ashley 2000).

San Miguel Island

San Miguel Island is the furthest west of all the islands, and its climate is characterized by perpetual northwest winds and prevalent fog (Figure 4). The topography of San Miguel is more diverse than Santa Barbara but is still rather moderate. Several small to medium-sized valleys radiate from one of two hills on the central and northwest parts of the island. Between the valleys are areas of gently sloping tablelands and flat areas. The west end of the island is very exposed to the wind and much of the land is or once was covered with sand. The

island coastline is characterized by many large beaches which support tens of thousands of pinnipeds during the winter.

Coreopsis stands, perennial grasslands, coastal bluff vegetation on cliff faces, riparian areas of willow and *Baccharis*, and scattered shrubs and chaparral stands likely comprised the historic vegetation of the island (Hochberg et al. 1979). Beach and coastal dune habitats certainly existed along the shoreline, but it is unknown how extensive these areas were before grazing began. It is estimated that during the peak of the sheep grazing era on San Miguel, up to 50% - 70% of the island was covered in sand (Hochberg et al. 1979). Today many of these interior dune areas are dominated by stands of lupine (*Lupinus albifrons*) and other native shrubs. Currently the island is mostly *Lupine* scrub, non-native annual grasses, and beach/dune vegetation.

Ranching began prior to 1850 with the arrival of sheep on the island. The numbers of sheep were never regulated, even when observers suggested that the sheep were destroying the vegetation. By 1862 there were already 6,000 sheep on the island, along with 200 cattle, 100 hogs, and 32 horses. Ranching continued for the next 100 years and caused significant damage to island systems. In addition, burros were brought to the island and were present from perhaps the 1940's to 1970's. The burros trampled vegetation, created trails, destroyed caliche and accelerated erosion until they were finally removed in 1978.

San Miguel is the only island in this study large enough to support a population of island foxes. The presence of foxes results in a system which certainly functions somewhat differently than the systems on islands without this terrestrial predator. Unfortunately this animal has very recently been removed from the system as the result of a drastic decline in its population to the point where all remaining animals (17) save one have been put in a captive facility while recovery efforts proceed. The effect of this situation on the mouse population on San Miguel will be discussed.

Methods

Deer mouse sampling using trap and release methodology is conducted in representative habitats as described in detail in the monitoring handbook (Fellers et al. 1988). Trapping grids (Figures 2-4) consist of 10 rows of 10 Sherman traps (H. B. Sherman Traps, Inc., Tallahassee, FL.) spaced 7 m apart. The traps are baited with oats and the grid is run for a minimum of three nights. Captured mice are marked with ear tags, examined for sex, age and weight characteristics, and released. Grids are normally sampled twice each year during spring and fall seasons.

Data analysis

Mouse monitoring

Estimates of population, density, and Mean Maximum Distance Moved (MMDM) are calculated by the program CAPTURE, a software package commonly used to statistically analyze data obtained in capture/recapture

studies (White et al. 1982). Program CAPTURE determines the most appropriate population estimation model from the data presented. Several of these models include robustness for variable capture probabilities, such as changes in capture success over time resulting from differences in behavior of the individual or changes in weather causing increases or decreases in total animals caught. The program recommends which model to use and then proceeds with analysis using the selected model unless directed otherwise.

For cases where CAPTURE was unable to calculate a density estimate, either because the total number of captures was too low or because the recapture rate was insufficient for analysis, densities were calculated using the total number of mice captured divided by the grid size plus one half the MMDM as a boundary strip width on all sides. For sampling sessions when total captures were too low for either method to provide an estimate, a density estimate of <10 mice/ha is included. This indicates that there were some animals present during the trapping period even though the capture rate was very low.

Vegetation monitoring

Specific measurements of vegetation composition are derived as explained in the vegetation monitoring protocol (Halvorson et al. 1988a). Data for this report were taken from the park's vegetation monitoring program (Johnson 1998, unpublished data, Channel Islands National Park). Vegetation monitoring is conducted via point intercept methods along permanent transects. Each transect is sampled annually, normally during the spring. Sampling was not conducted in 1989, 1991 or 1992. Every species which occurs at each predetermined point on the transect is recorded, as is the height of each individual plant at that point. From these data community descriptors such as species composition, frequency of occurrence, and cover type can be calculated.

For comparison of mouse data with vegetation characteristics we confined our analysis to the six of the mouse sampling grids for which there are vegetation monitoring transects immediately adjacent to the grid and in the same habitat. For two of the mouse grids on San Miguel no vegetation transect exists near enough to the grid to be descriptive of the grid

vegetation. In this report we analyzed summary vegetation data including the average heights of plants on each transect, the total number of individual plants encountered along each transect, the proportion of native and non-native individuals on each transect, and the percentage of herbaceous, shrub, subshrub, and grass vegetative forms for each year for those transects near the mouse grids in relation to mouse numbers.

To test whether or not mice impact survival of *Coreopsis* we examined data from the vegetation monitoring transect which is adjacent to the mouse grid located in *Coreopsis* habitat (#17) as well as two vegetation transects that are not in proximity to the mouse grid but are defined as being in *Coreopsis* habitat (#11 and #12). These two transects are in an area that was trapped by Collins et al. in 1978 and 1979, and at that time they estimated densities to be at least 240 mice/hectare during the three seasons they sampled (Collins et al. 1979). We made the assumption that when sampling on the TC grid results in high density estimates other *Coreopsis* habitats would likewise support high numbers of mice.

Murrelet egg predation

Estimates of numbers of murrelet eggs preyed on by mice were obtained from murrelet productivity data. Methodologies are described in the Seabird Monitoring Handbook (Lewis et al. 1988, Martin ed. In draft) and include recording the number of hatched versus broken eggs. Experienced observers can distinguish between the two, and according to the handbook any broken eggs are assumed to be mouse-eaten. For analysis of density and murrelet egg predation on Santa Barbara Island we averaged spring density estimates from the two mouse grids, or used one grid if only one was available.

Island fox densities

To monitor island foxes on San Miguel Island we used a standardized capture-recapture protocol developed specifically for island foxes, that has also been used on San Clemente, Santa Catalina, and Santa Cruz Islands (Roemer et al. 1994). We monitored island foxes annually in mid to late summer on three large (48 or 49-trap) grids, with distance between traps being 250 m. Live traps were baited with dry cat food and a fruit scent. Each

grid was trapped for six consecutive days, and traps were checked once during every 24-hr period. Annual adult population size was estimated for each grid using closed population models (program CAPTURE, version 2, White et al. 1982) as described by Roemer et al. (1994). To estimate annual islandwide population of adult foxes, average annual density from the three grids was multiplied by island area.

Raptor numbers

Raptors are counted according to methodologies in the Landbird Monitoring Protocol (van Riper et al. 1988) which directs that all birds seen or heard within 100 meters of the sample transects are recorded. We used only results from Santa Barbara Island for our analysis for two reasons. First, because Santa Barbara is so small, large birds that hunt there are assumed to range island-wide. This fact allows us to interpret changes in raptor counts as they may affect the entire island system. Additionally, Santa Barbara Island does not support black rats or island foxes, two species which, by their presence, affect mouse numbers and add variability to ecosystem patterns. We compared average mouse densities on the island with direct counts of mouse predators (American kestrel, northern harrier, short-eared owl, barn owl, and red-tailed hawk) in both spring and fall seasons when mouse densities and bird numbers were recorded.

Rainfall

Because conditions between the islands can vary significantly, rainfall data were obtained separately for the three islands. Data for San Miguel Island are taken from the daily weather observations taken by personnel on the island. Daily weather observations on Anacapa are not as consistent as on San Miguel, so weather data were obtained from the National Weather Service station in Oxnard, Ca, which is approximately 25 km from Anacapa. Santa Barbara Island is often unmanned, especially in the winter, so data from Catalina Island, approximately 50 km to the east, were used. An automated weather station on SBI has experienced sporadic maintenance problems so the data available from this station were not used.

Sampling grid locations

Figures 2, 3, and 4 show the locations of deer mouse sampling grids on the three islands studied identified by name and associated vegetation type. Mouse monitoring grids are located in different areas on the islands to allow sampling in representative habitats and geologic conditions, and were identified according to habitat type in the sampling protocol (Fellers et al. 1988). Two grids, the Dry Lake Bed (DLB) grid on San Miguel Island and the Inspiration Point grid (IP) on East Anacapa Island were not included in the original monitoring program. The DLB grid was established as part of a Master's Thesis project (David in prep.), and the IP grid was installed after mice were re-discovered on that islet in 1996.

Habitat descriptions

Coreopsis Scrub: Santa Barbara Island Terrace Coreopsis (TC grid)

Areas identified as *Coreopsis* habitat are often dominated by this native, semi-succulent shrub. *Coreopsis* plants grow to a height of about 2 meters, and are characterized by the abundance of bright yellow flowers which abound on the plant during the spring blooming period. Stalks of *Coreopsis* are quite fragile and are attractive food for mice. The understory of *Coreopsis* stands can be quite open or can include various assemblages of grasses and herbs. *Coreopsis* stands once covered vast areas of the islands, but were largely destroyed, particularly on Santa Barbara Island, during the times of non-native animal dominance. This community is expanding as the island gradually recovers from past grazing impacts.

Haplopappus (Isocoma) Scrub: San Miguel Island Airstrip (AS grid)

The airstrip grid is located in an area of low shrubs and grass, in a vegetation community dominated by the shrub now known as *Isocoma menziesii*, but identified previously as *Haplopappus venetus*. This species grows on poor, sandy soils, and is common on San Miguel Island in many of the areas where vegetation was previously scarce due to past land use. This community is unique among the three islands in this report. Other species commonly found in this habitat are *Ambrosia chamissonis*, *Astragalus migeulensis*, *Avena* spp. *Bromus*

spp. and *Dichelostemma capitatum*. There is no vegetation monitoring transect in this area.

Lupine Scrub: San Miguel Island Nidever Canyon (NC grid)

This habitat is characterized by the dominance of *Lupinus albifrons*, and on the Nidever Canyon mouse grid is accompanied by a significant understory of non-native iceplant, *Carpobrotus chilensis*. The north portion of this grid includes several patches of bare ground interspersed with small pockets of shrub assemblages, while the southern portion is thick with lupine shrubs up to 2m high. This grid is more structurally diverse than any of the others in the study.

Grassland: Santa Barbara Terrace Grassland (TG grid), Middle Anacapa Grassland (MA grid), West Anacapa Grassland (WA grid), San Miguel Willow Canyon (WC grid)

The specifics of grassland composition vary by island, but in general grasslands are characterized by the dominance of non-native wild oats (*Avena fatua*), brome grasses (*Bromus* spp.), and *Hordeum*. Native, perennial grasses can be associated with these exotic grasses, and natives are more common in the grasslands on Anacapa than on the other islands. Native and non-native shrubs have invaded the grasslands to some degree on all the islands, perhaps in response to the absence of fire in these communities. Other shrubs and forbs found in grasslands include *Erodium*, *Amsinckia*, *Dichelostemma*, *Coreopsis*, *Lycium californicum*, and *Artemisia californica*, and *Baccharis pilularis*.

Iceplant/Grassland: East Anacapa Inspiration Point (IP grid)

Non-native iceplant, *Mesembryanthemum crystallinum*, forms a thick carpet of succulent stems and leaves which can cover the ground to a depth of 30-40 cm. On the Inspiration Point grid this iceplant is interspersed with *Coreopsis* and various annual herbaceous and grass species.

RESULTS

Weights

We recorded weights for 7,365 mice over the study period. We restricted our analysis to adult male weights ($n = 3,375$) to remove the variability caused by inclusion of juvenile and subadult weights and weights of pregnant females. Adult male weights differed by season ($r^2 = 23.8$, $F = 350.212$, $p < 0.001$), decreasing from spring to fall on all islands (Figure 5). Adult male weights differed by island during the fall ($r^2 = 13.3$, $F = 161.177$, $p < 0.001$) and spring ($r^2 = 2.2$, $F = 8.015$, $p < 0.001$) seasons, being higher on Santa Barbara and lower on San Miguel in both cases. Population density had no effect on adult male weight ($n = 31$, $F = 0.035$, $p = 0.853$), nor did winter precipitation ($F = 0.539$, $p = 0.469$). The effect of previous winter's rainfall

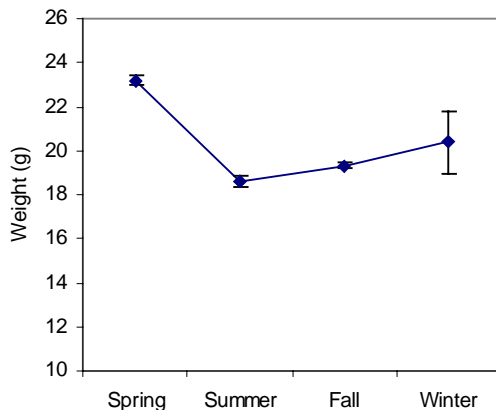


Figure 5. Average weights of adult male deer mice by season, 1992-2000, Channel Islands National Park.

(two winters previous) on fall adult male weights was weak ($r^2 = 10.1$) but almost significant ($n = 30$, $F = 3.142$, $p = 0.087$). To determine if dispersing mice weighed less than those which did not disperse, we compared the weights of adult male mice caught multiple times on a grid ($n = 1,379$) with those caught only once in a trapping session ($n = 2,123$). The average weight of mice caught once (19.9 g) was significantly less than average weight of mice caught multiple times (20.7g) ($t = 6.710$, $df =$

3500, $p < 0.001$), however this difference may not be biologically significant.

We compared adult male weights among grids to determine if habitat differences affected body condition. For this analysis we included weights from all seasons to incorporate annual changes in habitat quality. There were significant differences among grids on San Miguel Island but not on Anacapa or Santa Barbara islands (Figure 6). The highest weights

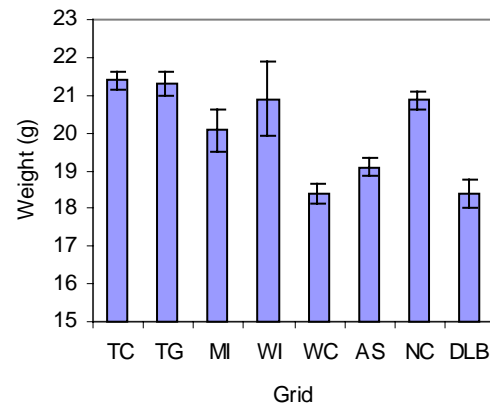


Figure 6. Average fall weights, with 95% confidence intervals, of adult male deer mice, Channel Islands National Park, 1992-2000.

island-wide were found on the Terrace *Coreopsis* (TC) and Terrace Grassland (TG) grids on Santa Barbara Island (mean = 21.4 g) and the lowest on the Willow Canyon grid on San Miguel Island (mean = 18.4 g). On San Miguel the average weights on the grassland grid (WC) were lower than in other habitat types and highest on the lupine scrub (NC) grid. On Santa Barbara Island weights on the grassland grid did not differ significantly from those on the *Coreopsis* grid.

Fall weights generally varied significantly between years. On Santa Barbara Island we examined average fall weights in all years in relation to population level changes (Figure 7). It is difficult to say from these data whether or not weights changed in response to cyclic periodicity. From 1993 to 1996 it appears that that may have been true; weights were

relatively low in 1993 when densities were very high and increased with an apparent population crash the following year. Weights then decreased over the next two years as the populations increased. However in later years there were no similar relationships.

Population and density estimates

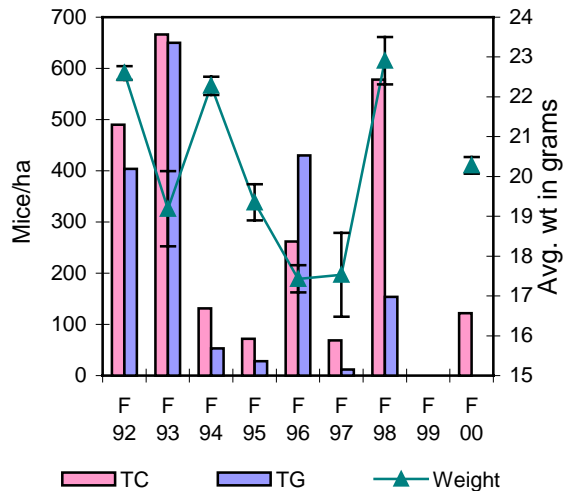


Figure 7. Deer mouse densities and average weights, Santa Barbara Island.

Estimates for mouse densities and population numbers, statistical parameters for estimates, calculations of mean maximum distance moved (MMDM), and numbers of captures for each trapping session are presented in Appendix 1. Unless otherwise indicated all estimates are taken from CAPTURE results, utilizing the model selected by the program. There were no instances when capture success was zero.

Variation in density

The highest sample density recorded was on the Nidever Canyon (NC) grid on San Miguel Island in October of 1998 with an estimate of 981/ha. Two additional samples, the Santa Barbara Terrace *Coreopsis* (TC) in October 1993, and the San Miguel Willow Canyon (WC) in October 1998 had over 650/ha each. The lowest densities were always recorded in the spring; on five occasions densities were estimated to be less than 10/ha: TC in March 1995, TG in March 1993 and 1999,

and West Anacapa (WAI) in March of 1993 and 1995. Overall within-island variability was the greatest on San Miguel Island, where densities ranged from 19/ha on the Airstrip (AS) grid in the spring of 2000 to 981/ha on the NC grid in fall 1998. On Santa Barbara Island densities ranged from <10/ha on the TG grid in the spring of 1993 and 1995, to 666/ha on the TC grid in the fall of 1993. On Anacapa densities ranged from <10/ha on the WAI grid, also in spring 1993 and 1995, to 318/ha on the Middle Anacapa (MAI) grid in the fall of 1995.

In several instances the increase in density from spring to fall was especially notable. On the TC grid in 1993 densities increased from 42/ha in the spring to 666/ha in the fall, an increase of almost 1500%. On the NC and WC grids in 1998 densities increased from 155/ha and 40/ha in the spring to 981/ha and 692/ha in the fall, increases of 537% and 1630% respectively. In a few instances densities decreased from spring to fall. On the TC grid on Santa Barbara in 1996 densities decreased from 402/ha to 262/ha. These spring densities were unusually high; numbers had in fact increased on the grid from the previous fall. Finally, on the TG grid in 1997, densities remained at a very low level from spring to fall, being estimated at 12/ha in both seasons.

There were no within-grid correlations between spring and fall densities, i.e. numbers of mice present in the spring do not, in themselves, determine fall maximums.

Density and precipitation

Winter rainfall during the previous season was positively correlated with spring densities on San Miguel ($r^2 = 74.6$, $F = 20.566$, $p = 0.003$) and Santa Barbara islands ($r^2 = 78.2$, $F = 17.910$, $p = 0.008$), and with all islands ($r^2 = 61.3$, $F = 28.457$, $p < 0.001$), but not with Anacapa Island ($r^2 = 47.0$, $F = 1.775$, $p = 0.314$). Previous seasonal rainfall was not correlated with fall densities in any instance. There was a weak but significant negative correlation of winter rainfall of the same year with spring densities on all islands ($r^2 = 26.3$, $F = 6.407$, $p = 0.021$), but no other relationship between current seasonal rainfall and spring or fall densities was found.

Vegetation condition

A weak but significant relationship ($r^2 = 24.9$, $F = 4.967$, $p = 0.042$) was found between spring mouse densities and the total number of vegetation hits recorded in the previous year. We observed no additional relationships between spring or fall mouse numbers and any other measurement of vegetation, including percentage of native species, grasses, shrubs, subshrubs, or herbaceous forms, average vegetation height, or total hits.

Density differences among habitat types

Santa Barbara Island

In all cases except one, when the two grids on Santa Barbara Island were sampled in the same season, the TC (*Coreopsis*) grid supported higher densities than the TG (grassland) grid. In years of low to moderate fall densities the TC grid supported relatively many more animals; in fall 1995 the density on the TC grid (72/ha) was three times the density on the TG grid (28/ha) (Figure 8). Again in 1997 when numbers were relatively low, the TC grid density (69/ha) was almost six times the TG grid density (12/ha). However in years when fall densities were extreme, the densities in the grassland increased to numbers much nearer to those in the *Coreopsis*; for example in fall 1992 densities were 490/ha on the TC and 404/ha on the TG grids.

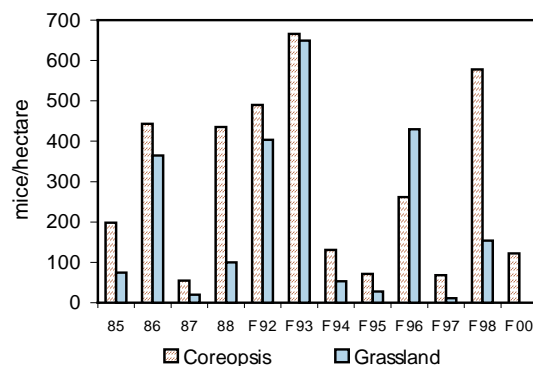


Figure 8. Fall deer mouse densities, Santa Barbara Island, 1985-2000.

San Miguel Island

Densities were always highest on the NC grid (lupine/iceplant) when this grid was included in spring sampling. In all cases when

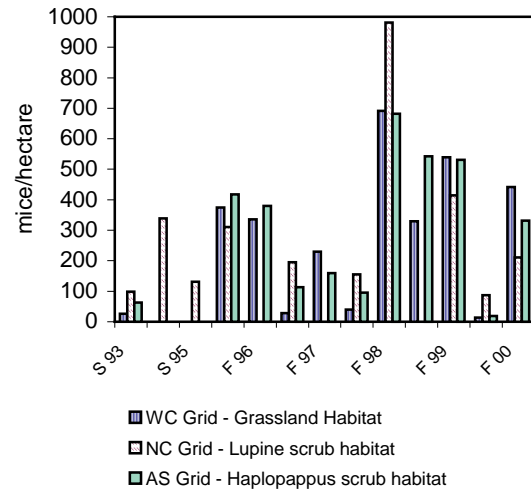


Figure 9. Deer mouse densities, San Miguel Island, 1993-2000.

the WC grid (grassland) was sampled in the spring, densities here were lower than in any other habitat. Habitat preference was apparently not as pronounced in the fall, and no one habitat type exhibited higher densities over all years. In contrast to Santa Barbara Island, grassland habitat on San Miguel Island (WC grid) often supported as many or more animals in the fall than did other habitat types (Figure 9).

Anacapa Island

The sampling grids on West and Middle Anacapa Islets are located in areas that are predominantly grassland. The Inspiration Point grid on East Anacapa, which is a mix of grassland, iceplant, and *Coreopsis* habitat, was only established in 1997 after the reappearance of mice on East Anacapa. During the few times that this grid has been sampled coincidentally with the Middle and West grids, density estimates have been once higher and twice lower than the grassland estimates on Middle Islet (Figure 10).

Mouse populations and other system components

We found no correlation between average spring mouse densities and depredation of murrelet eggs ($r^2 = 6.3$, $F = 0.267$, $p = 0.633$), however the sample size was small ($n = 6$). Removal of one outlier resulted in a strong, significant effect of mice numbers on murrelet egg predation. However, even at very low mouse numbers, predation was substantial (20-30%), and increased to less than 40% at extremely high mouse densities. There was a negative correlation between predation levels and murrelet productivity ($r^2 = 58.5$, $F = 8.442$, $p = .027$).

We found a negative relationship between fall mouse densities and total hits of *Coreopsis* in the following spring when we looked at transects 11 and 12, ($r^2 = 40.3$, $F = 8.109$, $p = 0.015$) but not with transect 17 ($r^2 = 48.5$, $F = 4.708$, $p = 0.082$) or with all three combined ($r^2 = 2.1$, $F = 0.652$, $p = 0.426$). Apparently high mouse densities in the fall resulted in less *Coreopsis* hits the following spring.

We found no correlation between direct counts of raptors on the three islands from 1993 - 2000 and mouse densities ($F = 0.408$, $p = 0.539$) on Santa Barbara Island, although the sample size was small ($n = 11$).

Dispersal

There were no correlations between the mean maximum distance moved (MMDM) and density. However, comparison of MMDM among seasons and islands showed significantly higher MMDM values in spring, compared to other seasons. Across all islands there was no significant relationship between the number of single captures and density ($F = 3.491$, $p = 0.066$), however this relationship was significant on San Miguel Island ($r^2 = 47.1$, $F = 11.135$, $p = 0.002$). There was no similar relationship between density and single captures on Santa Barbara Island ($F = 0.099$, $p = 0.757$).

No data on home range measurements are available from the monitoring program, however a current study on Anacapa to monitor effects of black rat removal on *Peromyscus* includes some radio telemetry data for mice.

Five radio collars were placed on adult male mice on Middle Anacapa in October of 1996, followed by the placement of collars on three additional mice in December of that year (Howald 1997). Population and home range estimates were obtained using methodologies described in the above report. Results indicated that the mean ranging area (90% MCP) was $137.6\text{m}^2 \pm 66.0\text{m}^2$ in October, and $179.1\text{m}^2 \pm 19.7\text{m}^2$ in December. MMDM was 7.35m in October and 14.07m in December (Howald 1997). The density estimates were 251/ha in October and 115/ha in December. These data are insufficient for statistical analysis, but are consistent with the theory that home range size increases as density decreases.

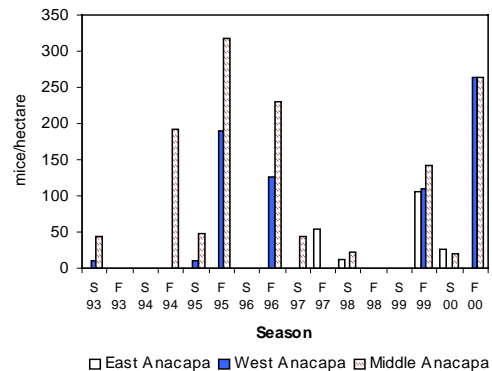


Figure 10. Deer mouse densities, Anacapa Island, 1993-2000.

DISCUSSION

Monitoring results

Population size

Our results support the conclusions of previous observers that populations of deer mice on the Channel Islands persist in exceptionally high numbers. The data also suggest that contrary to many other island systems which have been studied, the Channel Islands mouse populations experience recurring episodes of peaks and crashes in population size. An examination of our monitoring data, especially

when appended to results from previous island studies, strongly suggests that this is the normal state of these populations, particularly on Santa Barbara Island.

Given this situation it is probably unwise to define, as we might with other species, a range of values for population numbers of mice within which we would consider the population to be healthy. This is an interesting condition, given that one of the basic goals of a biological resource monitoring program is to determine such levels. There are however some seasonal generalizations that can be made from the data. Population densities in the spring are often very low, and capture rates of <0.02 per trapping session have been observed several times. Capture success has never been zero, but such an event occurring once during the spring probably would not be immediate cause for concern. We would assume that the few animals present were simply not trapped or were resident in areas adjacent to the trapping grid. However were this to occur on more than one grid in the same year we suggest that the situation would call for particular attention, and monthly trapping would be advised until animals were again detected. A capture success rate of zero during any fall session would be extremely unlikely on the islands, and would require immediate investigation.

Deer mouse densities on the Channel Islands ($<10/\text{ha}$ to $981/\text{ha}$) can be compared with a few studies from the Southern California mainland and other coastal island systems. Small mammal trapping in four habitats in the Santa Monica Mountains of Southern California in 1991 and 1992 (Schwemm 1993) resulted in density estimates for *P. maniculatus* of less than $10/\text{ha}$ in all habitats and throughout all seasons, even though they were sometimes relatively abundant. A similar study of vertebrate abundance in unmodified chaparral habitat resulted in an estimate of the average number of individuals for four *Peromyscus* species, including *P. maniculatus*, to be between 2.5 and 17.9 on 2, 150-meter long trap lines (Sauvajot 1997). Each of these studies was conducted in areas where *P. maniculatus* was only one component of a diverse small mammal community (between five and 10 rodent species were commonly trapped concurrently in each study.)

On the Gulf Islands off the coast of British Columbia, Sullivan (1977) found densities of *P. maniculatus* to average $22/\text{ha}$ on an island similar in size to Santa Barbara Island, and $43.5/\text{ha}$ on one equivalent in size to San Miguel Island. On Santa Cruz Island within Channel Islands National Park densities were less than $30/\text{ha}$ in all habitats during four seasons in 1994 and 1995 (Mayfield et al. 2000)

Rainfall appears to have two effects on mouse densities. High winter rainfall will encourage plant growth and provide food resources, however severe rains may increase mortality and reduce the numbers of mice surviving from fall to spring. The strong relationship between previous winter rainfall and following year spring densities suggests a multi-annual cycle which begins with winter rains. Spring plant growth responds to rainfall occurring between December and April, and most species will 'scatter' or drop seeds in late spring and early summer (K. McEachern pers. comm.) Mice will respond to available seed and plant resources with higher weights and greater reproductive activity. If food is available mice will continue to reproduce throughout the summer and into the fall; in a few cases we caught pregnant females in October and November.

It is apparent that rainfall is probably the most determinate factor in the regulation of mouse populations, however just how precipitation acts and to what extent the rainfall/vegetation relationship acts on mice is not clearly understood. The timing of rainfall is probably also very important in how it acts on the blooming and seeding cycle of plant species that serve as food resources for mice. More work is needed to better understand food habits and vegetation preferences of mice, and individual plant species responses to rainfall.

Population health

A measure of the general health of a vertebrate population is often derived from weight and reproductive data for the species. For this paper we have attempted to evaluate only weight information when determining the health of the mouse populations. Productivity data are difficult to collect within the scope of the monitoring protocol; most productivity studies require monthly or more frequent sampling throughout the breeding season. The monitoring protocol includes sampling only in spring and

fall, and in any case more frequent sampling would be extremely difficult with available personnel. The determination of age class is problematic when looking at juveniles and sub-adults, particularly when field personnel are volunteers or new to the species. Finally, while it often seems obvious that captured females are pregnant, there is no method in the field to confirm that fact, and large size females may in fact just be large. (We attempted to determine a weight limit over which females would be assumed to be pregnant, however we found that males often attained similar weight values.) Consequently we have not included productivity data here, and will be looking at future improvements to the protocol which will more easily provide such information.

Previous studies have shown that the average weights of a population will fluctuate as densities increase and decrease (Tamarin 1978, Krebs and Wingate 1985, Drost and Fellers 1991). For example a population in the increase phase of a cyclic pattern includes mostly healthy individuals. These animals are actively reproducing and healthy young animals are the result. As the population reaches peak density there are less resources available, aggression behaviors may increase, and more animals are forced to emigrate to less preferred habitats, resulting in lower individual weights. As the population declines less fit animals are lost to mortality and predation and stronger animals (those that weigh more) survive to begin the next increase phase. Because we found no obvious relationship between cyclic population patterns and weight changes on Santa Barbara

Island, it is possible that population levels, at least on that island, do not primarily determine individual fitness of mice. We suggest that these mice are so inured to living at high densities that the situation is not particularly stressful and does not generally affect individual fitness.

With long-term observations we can now suggest with some confidence the mean weight values for all groups in all seasons. If average weights fall below these limits in the future we will intensify our monitoring or turn to research to determine the causes of such variations from these means.

Ecology of Island Mice

Results from deer mouse monitoring suggest that these three island populations may be exhibiting population dynamic factors which differ in several characteristics from previously studied populations of rodents on other islands. This situation may be explained by a combination of intrinsic population characteristics and system factors unique to these islands.

Cyclicality

Measuring the periodicity of mouse population cycles is difficult. On Santa Barbara Island where data are most continuous, mouse densities apparently cycle with about a two to three year period between population peaks (Figure 11). On Anacapa Island data are not sufficient to detect any cyclic patterns that may exist, however there are some indications that Anacapa populations experienced peaks during the same years as were observed on Santa Barbara. The situation on San Miguel is impossible to analyze for natural cyclic patterns during this period because of the removal of the fox from the system. Any apparent increases in populations that could previously have been attributed to an increase phase of a cycle is more likely due to the release of predation pressures, as will be discussed below.

Individual weights of animals on Santa Barbara Island, where cyclic population patterns are most pronounced, did not appear to fluctuate in concert with cyclic periods. Identifying cyclic patterns is somewhat subjective, however from the data we can suggest that increases occurred sometime prior to 1992, 1994-1996, 1997-1998, and 1999-2000. Changes in mean weights

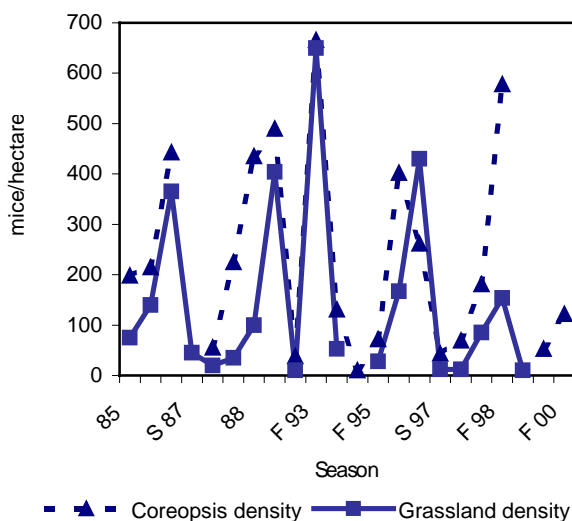


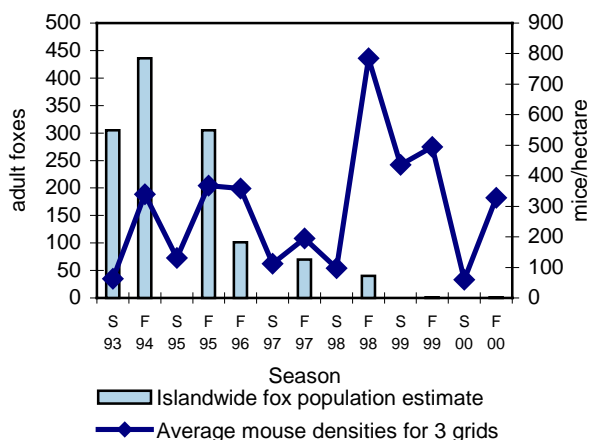
Figure 11. Change in deer mouse density over time, Santa Barbara Island, 1985-2000. (Data 85-88 from Drost and Fellers 1991.)

island-wide showed no similar patterns, i.e. it does appear that weights increased following population crashes. For example, in the fall of 1997, the population appears to have been recovering from a crash from the previous high in 1996. If this were true, we would expect weights to be increasing as the healthy animals surviving the crash continued to produce healthy young with little competition for space and food. However the mean weight in the fall of 1996 was actually higher than in the following year. Likewise, an apparent upward trend in the fall of 1995 showed weights lower than the previous fall when densities were higher and the population was apparently recovering from the extreme high numbers noted in 1993, when densities were the highest ever measured on Santa Barbara.

Regulating mechanisms – Predation

The highest densities recorded during this study were from San Miguel Island in 1998, and are as high or higher than previously recorded in the literature for this species. It appeared that the explosion in deer mouse numbers on San Miguel Island was a response by the mouse populations to the disappearance of the island fox from the system. The population of foxes dropped from what we believe to be a close to normal level of approximately 6-10 foxes/km² to no wild foxes on the island within a period of about four years (Coonan et al. 1998) (Figure 12). Such a swift decline of a primary predator from a natural system is probably rare, and therefore quite interesting in terms of the response of the prey species.

Island foxes are generalists that feed on a variety of food items (Laughrin 1977, Collins



and Laughrin 1979, Collins 1980, Roemer 1999). On Santa Cruz Island mice were more commonly taken as prey during winter and spring months when other food sources were more scarce, but were eaten by foxes in all seasons (Laughrin 1977). On San Miguel Island Collins and Laughrin (1979) reported deer mice comprised 53 percent of the fox scats analyzed in the winter, decreasing to 2 percent in the summer. David (in prep.) found deer mice in 76.8 percent of all fox scat analyzed from 1993-1998 on San Miguel Island, and in 100 percent of all samples during 1996. Collins and Laughrin suggested that mice are an important food item for San Miguel foxes (1979), and David's preliminary work certainly seems to support this assessment (David in prep.) Because of the numbers of mice taken by foxes before the fox decline, we suggest that predation by foxes was by far the strongest regulating mechanism acting on mouse populations on San Miguel Island. When the foxes were removed from the system, other intrinsic regulating mechanisms that might have been present were unavailable, and mouse numbers increased far above historic levels.

Mouse behavior likely changed as the ecology of San Miguel Island transformed. For example, there was a correlation between population density and the number of single captures on San Miguel that was not noted on the other islands. This suggests that mice on San Miguel are not as tolerant of high densities as are mice on the other islands, and when mouse populations increased as a result of fox demise, individual mice were driven to disperse with greater frequency than were the more tolerant mice on Santa Barbara and Anacapa islands.

Because both Anacapa and Santa Barbara islands lack island foxes but support a similar suite of aerial predators, the predation pressures on mice are likely comparable between the two islands. Drost and Fellers (1989) suggested that aerial predation was the dominant process limiting mouse populations on Santa Barbara Island. According to their observations, significant predation by raptors during peak years resulted in subsequent population declines, and functioned to regulate the mouse population on a 3-4 year cycle.

The predation data collected during their study were much more descriptive than information available for the period of this study,

Figure 12. Islandwide fox population and deer mouse densities, San Miguel Island, 1993-2000.

however data collected by the landbird monitoring program provide a general index of observations of predatory bird species. Relationships between mice and aerial predators are certainly more complex than would be identified by this analysis, but our results from Santa Barbara Island suggest that high numbers of predatory birds on the island does not immediately result in mouse declines. It is more likely that, as Drost and Fellers (1991) suggested, a dynamic relationship exists between these two groups, and an increased prey base may draw predators to the island, while reduced mouse numbers cause birds to return to the mainland or the larger islands to forage. Also, we did not look at specific changes in bird species; certainly some raptors take more mice per individual than do others.

Finally, it has been suggested that although the land bird monitoring protocol adequately provides relative abundance data, it does not estimate absolute abundance (Channel Islands National Park Land Bird Protocol Review internal documents, 2000) as deer mouse sampling does. Consequently, the lack of an observed relationship between mouse numbers and raptor abundance may be misleading. More investigation is needed to understand the degree to which populations of raptors and deer mice on Santa Barbara Island are interrelated.

Predation of mice by seabirds is almost certainly not existent at high enough levels to function as a system regulator, however it may be a process that is significant in localized and occasional situations. Western gulls nest in large numbers on Santa Barbara and Anacapa islands and are sometimes observed eating mice that wander too close to nesting areas (P. Martin pers. comm.) While not usually considered a predator of mice, in years when mouse populations are low and gull numbers are up, predation by gulls may affect mouse numbers.

The most significant difference between the two islands is the presence of black rats on Anacapa. Direct predation of mice by rats has been observed on the Channel Islands. Collins et al. (1979) noted that rats apparently ate mice on several occasions when the two species were caught in the same trap and Gellerman (pers. comm.) has seen several instances of rats carrying mice in their mouths. Although rats almost certainly reduce mouse survival on the islands where the two species coexist, it is

unknown whether or not direct predation on mice by rats has any significant impact on mouse numbers.

Regulating mechanisms – Space

Abundant food, mild weather, lack of predators and competitors, and optimal habitat on the Channel Islands apparently combine to produce one of the most hospitable environments for deer mice anywhere in the world. The fact that there were no within-grid correlations between densities in spring and those in the following fall on any island suggests that external environmental factors are largely responsible for population regulation. Even a small number of individuals alive in the spring, when provided with an optimal suite of environmental variables, can apparently reproduce continuously throughout the season. Reproduction will cease in such a year only when some environmental or ecological limits are reached.

So many factors of island ecology are favorable to mice that in years when mouse numbers reach such exceptional levels it may be that the only regulator of density is actual physical space. Support for the theory that there are almost no internal regulating factors of mice on these islands can be found by examining the current situation on San Miguel Island. Apparently predation by foxes was the most significant restraint on mouse populations up until this time, and when foxes were removed from the system there were few intrinsic mechanisms in place to limit mouse numbers.

It has been suggested that habitat space available to mice may be limited by the effect of seabird nesting colonies on mouse densities. Santa Barbara and Anacapa islands are relatively small, and seabird productivity, particularly of the species that nest in large colonies such as brown pelicans and western gulls, has generally increased within the last ten years (Martin and Sydeman 1998, Martin et al. 2001, unpublished Channel Islands National Park seabird monitoring data). Each of these islands is host to thousands of nesting seabirds during the early spring and throughout the summer. Within the gull colonies there is very little suitable habitat for mice during the nesting period, due to gull nesting behavior and denudement of nesting areas. While gulls don't actively hunt mice, they will prey on them

opportunistically in those areas. It is unclear how mice respond to brown pelican nesting activities. They may utilize the large nests built by pelicans for cover or nesting areas of their own (P. Martin pers. comm.), however pelicans by their size and habits may also be intimidating to mice and may discourage mice from entering those areas during nesting and chick rearing periods.

The sampling grids for mice are not located in areas of high nesting activity, but will likely receive mice that are displaced from bird colonies. Interestingly, while populations of nesting seabirds have increased dramatically over the last decade, there do not appear to be higher mouse densities on our study sites as a result. On Santa Barbara Island the population size of western gulls increased in 1997, 1998 and 1999 (Martin and Sydeman 1998, Martin et al. 2001, unpublished Channel Islands National Park seabird monitoring data), however mouse densities were very low in 1999, about 100/ha in 1998, and between those numbers in 1998. It may be that while areas made unavailable to mice by seabird nesting activity are increasing, the amount of good quality habitat in other areas is increasing due to recovery of native habitat, particularly stands of *Coreopsis*.

Other than areas that may be made uninhabitable by seabird nesting activities, it appears that all other areas, aside from bare rock, likely support some numbers of mice. Previous studies have shown that in the absence of interspecific competition *Peromyscus* may be found in almost all habitats, and are not limited by the structure and composition of the vegetation (Baker 1968 for review). On the islands this suggestion is supported by the fact that trapping in all habitats is successful. Deer mice are extremely opportunistic in their feeding behavior as well, and eat a wide variety of seeds, fruits and mast (Collins et al. 1979), and the islands provide ample sources of all these foods. This combination of abundant food and habitat resources suggests that habitat quality is measured by mice only in terms of relative desirability. No vegetated area on the islands is considered bad habitat by mice; some of it is just less good. And even habitat that may in some years be sub-optimal will, in years of high vegetative productivity, support great numbers of mice. Only when the physical space is saturated with mice will reproduction cease.

Regulating mechanisms - Dispersal

In most small mammal species, when population densities are high, increased dispersal out of crowded areas is normally observed (Lidicker 1975; Tamarin 1978; Gaines and McClenaghan 1980; Wolff 1985). Because island populations of mice routinely survive at extremely high numbers, one could suggest that individuals within those populations are more adapted to existing under crowded conditions and are less stimulated to leave good habitat simply because less space is available. We found no change in MMDM when densities increase, suggesting that island mice do in fact tolerate much higher densities. Apparently populations can get very high before the stimulus to leave an area is triggered. Individuals who leave an area appear to be slightly less fit than those that remain; animals that were caught only once (transients) weighed an average of 0.8 g less than those caught more than once (residents).

MMDM was greatest in the spring, although it was not specifically correlated with low density. During the spring animals will travel greater distances to find scarce food resources and potential mates. As mentioned, there is no significant relationship between higher densities and lower MMDM, so as densities increase, the dispersal behavior which is triggered by reduced living space appears to be somewhat tempered by proximity of available food and mates. We also found no relationship between density and the ratio of single captures to multiple captures on Santa Barbara or Anacapa islands, again suggesting that dispersal on these islands does not increase at higher densities. The situation on San Miguel is unique and has been discussed above.

Regulating mechanisms – Behavior

Several studies have suggested that insular populations of *Peromyscus* are less aggressive than comparable mainland populations (Halpin and Sullivan 1978, Halpin 1981, Mossman and Srivastava 1999). If true, such a condition is likely an adaptation to the stresses of living in close proximity to many conspecifics, and corresponds to other evolutionary changes in island populations in response to insular processes. Unfortunately

Table 1. Single and multiple captures of deer mice in traps, by island and year.

Island/Year	Single captures	Double captures	Three or more captures
Santa Barbara Island			
1993	391	78	2
1994	167	2	
1995	37	10	
1996	531	45	1
1997	98	1	
1998	137	1	
1999	16	0	
Anacapa Island			
1993	37	0	
1994	63	9	
1995	226	17	
1996	138	4	1
1997	141	2	
1998	42	1	
San Miguel Island			
1993	201	5	
1994	168	28	
1995	627	92	3
1996	426	84	1
1997	1069	108	1
1998	1124	244	16, 4 with four, and 1 with five
1999	1005	140	6, 1 with four
2000	822	109	3

very little work has been conducted regarding the behavior of Channel Islands mice. We have only two anecdotal observations that may support the suggestion of reduced aggression in these populations.

First, we have noticed very few indications of aggressive interactions between individuals. When handling mice, particularly during the breeding season, we have rarely seen injuries that might occur between individuals living in stressful conditions. Agonistic behaviors most commonly occur between two breeding males or between a

breeding female and any other adult, and are usually triggered when an animal enters the territory of another (Eisenberg 1968, Wolff 1989 for reviews). As density increases these territories become more numerous, and more such interactions must logically occur. Because we see few actual injuries, it appears that these types of territorial infringements do not trigger aggression at levels seen in other populations.

Secondly, we often caught two and even three or more individuals in one trap (Table 1). The nature of the traps dictates that for more than one individual to be caught the animals

must be travelling very closely together. This would be common for an adult and a juvenile, but in many cases these animals are all adults, although their relationship to each other is unknown. The most dramatic examples of this phenomenon occurred on San Miguel Island in 1998 and 1999. During the fall seasons of those years mouse densities were extreme, and in several cases three, four and even five individuals were found alive in closed traps. The thought of how this could have occurred has been the topic of humorous discussion, but regardless of the means, in over 30 instances three or more animals all entered traps in very close proximity to each other and survived without serious aggressive behaviors throughout the night.

Habitat relationships

Habitat use by mice appears to be selective and varies with population changes. Results from sampling suggest that during years with low to moderate densities mice are free to select habitats of choice. The absence of interspecific competitors results in almost unrestricted access by mice to any desired area. (In a few areas nesting seabirds may prevent utilization of some areas during particular seasons, as was mentioned above.) However in years when densities exceed capacity in preferred habitats, these areas may function as reservoirs of individuals that emigrate to less optimal habitats.

An example of such a situation appears to exist on Santa Barbara Island between the TC (*Coreopsis*) grid and the TG (grassland) grid. When densities are high, mice will occupy grassland areas in greater numbers as they are driven to leave the saturated *Coreopsis* habitat. In most systems this dispersal would be tempered by the presence of interspecific competitors in the destination habitat (Grant 1975, Scott and Dueser 1992). The lack of any such species on the Channel Islands, combined with the relative quality of grasslands as mouse habitat, determines that in good years dispersing individuals will occupy 'second-choice' habitat in almost as high densities as the habitat they have left. In this case the grassland area should not be considered a sink habitat; grasslands are capable of supporting very high numbers of animals and there is no indication that mortality increases in this area.

Mice trapped on the Santa Barbara TG grid did however weigh marginally (0.8 g) less than those on the TC grid, suggesting that the animals here are somewhat less fit when they arrive, or have reduced access to food resources. Because this difference is so small, it is more likely that some factor of habitat structure is less preferred and food is not lacking. The obvious difference between the habitats is the amount and structure of cover. On Santa Barbara mice need only hide from aerial predators, so it is likely that *Coreopsis* plants provide better protective canopy than do grasses. This makes intuitive sense, but we have no evidence that this is true. Areas of *Coreopsis* on Santa Barbara Island apparently provide the better combination of variables than do grassland areas, but the degree of preference appears to be relatively small.

However if it is the case that food is not particularly limited in the grasslands on Santa Barbara, and if grasslands are similar across the islands, then we would expect that average weights from the grasslands on San Miguel would be close to those in other habitats. (The only grid on Anacapa that is not in grassland habitat has been sampled for only two years so no comparisons are possible.) This is not the case, and weights from the WC grid are significantly less than either the AS (*Haplopappus* scrub) or NC (lupine/iceplant) grids ($F = 83.24$, $p < .001$). The difference in means between the WC and the AS grid was weak but significant (0.69 g), however the difference between the WC and the NC grid was highly significant (2.46 g). These differences were certainly affected by the anomalous data from 1997 when winter precipitation was very low and weights for the WC grid averaged only 15.52 g. Densities on the WC grid during that period were abundant (230/ha) and were higher than densities on the AS grid, but were lower than during any previous or subsequent fall sampling on that grid. The fact that the AS grid supported fewer but healthier mice suggests that the grassland is normally good habitat but was particularly impacted by lack of rain and did not provide adequate food resources during this period. It is suggested that during periods of low rain, the grasslands on San Miguel will be more negatively affected, hence the more dramatic response in mouse weights on the respective islands.

Drost and Fellers (1991) suggested that on Santa Barbara Island grasslands were at all times the less preferred habitat. If we expand their findings from Santa Barbara to the other islands, and assume that grasslands function as mouse habitat in a similar manner on all the islands, we might assume that grasslands are a less productive habitat on all islands. This appears to be true on Santa Cruz Island, where a study conducted in 1994-1995 found virtually no mice in grassland habitat during any of four sampling periods, including September and December of 1994 (Mayfield et al. 2000). Mice were found in other habitat types during this period but never in high numbers. These results are in extreme contrast to those from Anacapa Island during the same period, when mouse numbers in grassland were estimated at 192/ha in October (Schwemm 1996). Anacapa and Santa Cruz are only about 10 km apart, so it is unlikely that weather during this period was responsible for a significant difference in habitat quality between the grassland areas on the two islands. And because grasslands are the only habitat types sampled on Anacapa, we do not know whether densities in other areas would have been comparably higher during this period as they were on Santa Cruz Island.

This situation on Santa Cruz was very likely affected by the predation regime created by the presence of the island fox. A current investigation is examining the different foraging strategies of the fox on Santa Cruz Island (Roemer and Schwemm in prep.), and may suggest that mice are selectively hunted in grassland areas, thus resulting in lower densities in grasslands on Santa Cruz and San Miguel where foxes are present, but not on the smaller islands where foxes are absent. It may also be true that grasslands as mouse habitat are much less productive during periods of low precipitation but during wet years are much more comparable to other habitat types.

Variability in habitat composition

We were interested in knowing whether data from spring vegetation monitoring might be useful in predicting fall mouse densities. We found no correlation between any vegetation measurement of plant life form on the transects adjacent to mouse sampling grids and spring or fall mouse densities. The vegetation monitoring program defines plant life forms as grass, herbaceous, shrub, and subshrub; changes in

the percentages of these plant types apparently had no effect on mouse densities.

Coreopsis

Despite the apparent negative relationship between fall mouse numbers and spring *Coreopsis* productivity, *Coreopsis* is increasing in distribution on Santa Barbara Island (Figure 13). *Coreopsis* stands were almost eliminated during the period when rabbits were abundant on the island but have responded well to the removal of the rabbits. In 1997 a severe windstorm resulted in a significant blow-down in the *Coreopsis* stand (#17) adjacent to the TC mouse grid, and biologists monitoring the stand in the spring of 1998 made note of the many toppled plants (Channel Islands National Park vegetation monitoring data). Apparently the location of this

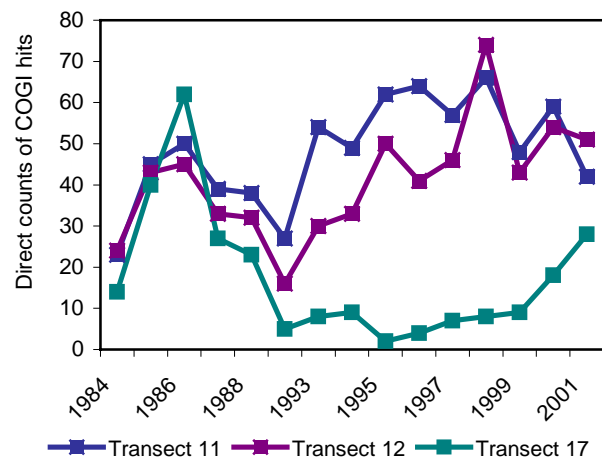


Figure 13. Abundance of *Coreopsis gigantea* on three transects, Santa Barbara Island, 1992-2000.

stand made it particularly vulnerable to the winds, since two stands on the north side of the island did not experience the same damage (#11 & #12). Mouse numbers on the TC grid in the fall of 1997 were relatively low (69/ha); if mouse numbers had been higher that year their impact on the damaged stand may have been much greater. As it was, the stand recovered, and the numbers of *Coreopsis* plants has increased every year since. Apparently even with extreme mouse densities and resulting predation by mice on *Coreopsis*, the productivity of this plant is not regulated in the long-term by mice.

Mouse effects on seabirds

Mice have been shown to prey upon seabird eggs, and particularly murrelets, on both Anacapa and Santa Barbara Island, however no quantitative relationship has been established between mouse numbers and amount of seabird predation. We suggest that in years when spring mouse densities are high there are also additional food resources available to mice, resulting in relatively less predation on murrelet eggs. Also, there may be differences in the dynamics of the subpopulations that live near the bird colony that cause them to function differently. No research has been conducted to determine whether or not murrelet eggs are a preferred food source for mice, but it is certainly likely. The proximity of this additional food source may therefore have some regulating effects; if eggs are particularly nutritious, significant intake of egg material by mice may result in mouse productivity that is higher in this area than on other parts of the island.

Most bird and mouse researchers agree that mouse sampling near the murrelet nesting colonies on Santa Barbara Island would provide extremely useful information. Unfortunately the conditions that provide good murrelet habitat preclude mouse trapping (steep areas, unstable cliffs). Mouse trapping in the spring would also cause disturbance during the bird nesting period, which is undesirable. Finally, considering that mice are native to the system, mouse impacts to murrelets, whatever they may be, have and will continue to occur. This is an unfortunate situation for the murrelets, which are threatened by many other factors that originate off-island.

NPS Management Issues

Anacapa recolonization

The causes of the disappearance of mice from East Anacapa for almost twenty years are still unknown. One possibility is that the population experienced several years of a downward trend, similar to what we have observed on Santa Barbara Island, but was unable to rebound and increase productivity due to the presence of rats. Rats may have acted to directly reduce mouse numbers through

predation, but that scenario is unlikely. It is more probable that rats function as aggressive competitors to mice and occupy prime habitats. Although they were probably not directly responsible for the initial mouse population decline, it is very likely that they prevented substantive recruitment.

We have also shown that Channel Islands mice are less prone to dispersal than are mice in other environments. If this is true, once mice were eliminated from East Island it may have taken just the right combination of factors on Middle Island to stimulate a few individuals from that population to venture across the water to East Island. We have shown that on Santa Barbara Island mice are extremely tolerant of high densities. If this is the case on Anacapa as well, even very high densities on Middle Island may not have prompted such behavior. Because we have very little density data from Middle Anacapa Island from any period prior to 1993, we don't know what the population levels were on that island between the time mice left East Island and the time they returned in 1996. Densities in the fall of 1995 on Middle Island were estimated to have been 318/ha, which is certainly quite high, but only about average for fall densities on the Channel Islands. We examined tide data from 1994-1996 for any indication that an extreme low tide event may have initiated dispersal activity from Middle to East Anacapa, but found no records of such an event.

Whatever the reasons for the disappearance of the mice from East Anacapa, two conclusions can be made from this occurrence that should be kept in mind in future management activities. First, it appears from this situation that it is possible for deer mice to be eliminated from a small island by natural causes. There is no indication that the loss of the mice was due to human activities (other than the introduction of rats); more likely there was some combination of physical and biological factors which drove the East Anacapa population to extinction. As stewards of the resource, the park must be mindful that such an extinction could happen again, and continue to monitor and observe the mouse populations, particularly on the smaller islands.

Secondly, the deer mouse populations on the three Anacapa islets may be an example of a naturally - occurring metapopulation, with

sub-populations occurring on each islet. It is likely that a single sub-population cannot exist in the long-term without the existence of the others. The similarities and differences between naturally-occurring and human-caused metapopulations have been studied extensively. Results from such studies have provided information useful in the understanding and preservation of populations in human-created patchy environments where the loss of habitat to development has created island-like areas that support sub-populations of species that were once continuous. We suggest that there is a great deal more information to be gained by the study of the Anacapa populations, both alone and in comparison with the other islands, that may be useful in the larger effort to protect small mammal populations such as these in urban environments.

Implications for rat removal activities on Anacapa Island

Preliminary tests of the baiting protocol for black rat removal on Anacapa Island conducted in November, 2000 have determined that mortality effects on mice in the targeted area are probably close to 100% (G. Howald pers. comm.). These results were expected, and should not prevent the project from moving forward. Aerial baiting of East Anacapa is planned for the fall of 2001 and it is likely that mice will be eliminated from that island as a result of the bait application. Alternatives for mouse removal prior to the application and subsequent reintroduction have not been specifically outlined in the Environmental Impact Statement (Channel Islands National Park, October 2000). As a result of our findings in this paper we suggest the following points be kept in mind when determining the final mouse preservation strategies for the project:

- Generally, significant reproduction in deer mice on the islands does not occur between late fall and spring. If mice were removed from East Island and transported to West Island immediately prior to the November-December bait application, it is likely that very little mating would occur between the transplanted animals and the residents. If these mice were tagged, reasonable trapping efforts would likely result in a fairly high recapture rate of those surviving the winter, allowing these mice to be returned to East Island. While it has been determined

that there are probably no significant genetic differences between the islet populations (O.R.V. Pergams and M. Ashley pers. comm.), it would be preferable to maintain the different populations as much as possible. A similar protocol could be implemented when Middle and West islets are treated, although the number of mice temporarily relocated to East islet would need to be much greater. Such a relocation of individuals into an existing population will certainly have some negative effects on resident mice during this period, however such impacts would be temporary.

- Removal of mice from the island to an off-site facility is probably unnecessary given the cost and the risk. In most years there will be enough mice on West and Middle islands to allow the removal during the breeding season of enough individuals to repopulate East Island in only a couple of years. We can look at the recolonization which recently occurred on East Island to feel confident that this is true. However because there is a relationship between winter weather and survival, it is possible that the winter following the elimination of mice on East Island would be severe enough to significantly reduce the populations on the other islets, eliminating the flexibility of removing excess animals from those islands. If that were the case, the postponement of the treatment of Middle and West islets for one year might be considered. On-island holding of mice should also be considered as a source of animals for reintroduction to East Anacapa.
- The process by which mice are returned to East Island following their elimination should be carefully planned, and reintroduction strategies should be designed to maximize the research potential. When mice returned in 1996 we were not expecting it and hence were not prepared to monitor the recolonization as it occurred. In this case valuable information regarding dispersal, habitat use, rate of recruitment and other ecological variables should be obtained by means of a study plan which aims to measure these factors.

Conservation of Xantus' murrelets on Santa Barbara Island

Predation by deer mice is negatively affecting the productivity of Xantus' murrelets on Santa Barbara Island and consequently should be considered a threat to overall murrelet population survival. It may be possible to mitigate these losses by removing mice from areas surrounding the murrelet breeding colonies during the nesting season. Based on the information presented in this report we suggest that such a localized reduction, if conducted in the following manner, would very likely have no significant long-term impacts on the status of the deer mouse population on the island.

- 1) Live trap or snap trap lines would be established around the murrelet nesting colonies. These colonies are located in areas between the upper terraces of the island and the water's edge, so it might be possible to completely surround the colony with a line of traps between the main island area and the water. If snap traps are determined to be unusable because of dangers to non-target species, particularly

birds, mice could be euthanized after capture in live traps. This trapping would begin with the first observance of eggs in nests and would end as soon as all surviving chicks are gone from the island.

- 2) Regardless of the method of capture, all mice that are caught will be sexed and aged, and live animals will be weighed. While this would be primarily a reduction effort, the capture of additional mice outside the established sampling grids would add information on mouse demographics to that collected during monitoring.
- 3) This project would require environmental documentation and would be coordinated by the seabird monitoring biologist at the park. The decision to undertake these efforts would be made by the interested biologists within the seabird community, and would only be undertaken if that group determined that the potential protection that would be afforded the murrelets would outweigh the additional seasonal effort that would be required to establish and maintain these trap lines.

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APPENDIX 1. RESULTS OF DEER MOUSE POPULATION MONITORING

Island	Grid	Date	Total Indiv.	Total Captures (Prob. of capture)	Selected Model	Pop. Estimate (95 % C. I.)	MMDM	Density mice/ha	S.E.
Santa Barbara	TC	9/92	231	353 (.40)	M (o)	294 (267-321)	.76	490	75.6
		3/93	20	45 (.75)	M (o)	20 (18-22)	1.92	42	6.6
		10/93	208	332 (.36)	M (h)	308 (279-337)	.77	666	88.2
		9/94	48	96 (.64)	M (o)	50 (46-54)	1.08	131	23.0
		3/95	3	8				10	
		11/95	31	32				72	
		3/96	131	205 (.42)	M (o)	162 (149-184)	.84	402	60.5
		10/96	127	162 (.26)	M (h)	212 (190-242)	.71	262	57.8
		3/97	19	30 (.45)	M (t)	21 (17-25)	1.38	43	15.4
		10/97	27	35 (.26)	M (o)	45 (24-66)	1.11	69	66.5
		4/98	50	66 (.27)	M (o)	81 (55-107)	1.33	181	73.4
		11/98	162	184 (.20)	M (h)	301 (284-318)	.56	578	94.8
		3/99	2	5				10	
		4/00	43	92 (.48)	M (b)	50 (38-62)	1.43	53	38.1
		8/00	186	285 (.40)	M (o)	236 (212-260)	.55	356	66.5
		10/00	122	211 (.31)	M (o)	124 (97-151)* 8x8 grid	.6	642	158.4
		3/01	141	215 (.4)	M (bh)	180 (159-201)	.49	290	60.0
Santa Barbara	TG	9/92	224	456 (.42)	M (bh)	265 (236-294)	1.77	404	93.6
		3/93	6	9				10	
		7/93	144	181 (.22)	M (t)	226 (205-327)	.86	650	194.9
		6/94	41	48 (.07)	M (t)	83 (40-126)	.33	122	190
		11/94	19	25 (.56)	M (t)	25(16-34)	1.33	53	23
		11/95	12	14 (.17)	M (o)	28 (0-57)	3.04	28	14.7
		3/96	100	146 (.11)	M (o)	135 (118-161)	.86	167	52.9

DEER MOUSE TREND REPORT

Island	Grid	Date	Total Indiv.	Total Captures (Prob. of capture)	Selected Model	Pop. Estimate (95 % C. I.)	MMDM	Density mice/ha	S.E.
Santa Barbara	TG	10/96	84	101 (.18)	M (t)	172 (130-252)	.58	430	228.1
		3/97	14	23 (.49)	M (o)	16 (11-21)	1.84	12	5.8
		10/97	12	16 (.63)	M (o)	18 (7-29)	.5	12	2.6
		4/98	48	72 (.41)	M (t)	55 (46-64)	.28	85	17.7
		11/98	46	53 (.21)	M (h)	83 (66-101)	.29	154	47.6
		3/99	1	2				10	
W. Anacapa	Grassland (WA1)	3/93	6	7				10	
		3/95	4	7				10	
		11/95	91	135 (.38)	M (o)	120 (101-139)	.77	190	54.2
		10/96	24	45 (.60)	M (o)	26 (25-32)	1.61	127	21.7
		11/00 ^	124	154 (?)		243 (179-307)		265	176.0
	Slope (WA 2)	10/96 ^	41	74 (.56)	M (o)	44 (38-50)	1.03	169	31.4
		12/99 ^	68	118 (.33)	M (b)	97 (56-138)	1.74	111	90.2
M. Anacapa	Grassland (MA 1)	3/93	17	26 (.73)	M (o)	18 (14-22)	1.72	45	10.9
		10/94	59	81 (.60)	M (t)	77 (61-93)	.9	192	57.2
		4/95	17	26 (.42)	M (o)	21 (14-28)	.9	49	29.5
		11/95	75	93 (.21)	M (o)	147 (97-197)	1.71	318	146.7
		10/96	53	100 (.59)	M (o)	56 (54-65)	1.05	230	23.9
		3/97	11	15	M (o)	15 (6-24)	2.33	45.3	26.0
		4/98	16	22 (.32)	M (o)	23 (12-34)	2.16	22	17.7
		12/99	70	124 (.27)	M (b)	114 (48-180)	1.72	142	132.4
		3/00	12	24 (.67)	M (o)	12 (10-14)	1.14	20	6.2
		6/00 ^	54	95 (.53)		60 (53-67)		90	15.0
		7/00 ^	86	137 (.44)		104 (90-118)		173	31.8
		8/00 ^	119	214 (.55)		131 (121-141)		129	22.8
		9/00 ^	143	278 (.61)		151 (143-159)		234	16.7
		11/00 ^	109	151 (.31)		161 (131-191)		264	126.5
E. Anacapa	IP (EA 1)	11/97	24	44 (.58)	M (o)	25 (21-29)	1.35	54	10.2

DEER MOUSE TREND REPORT

Island	Grid	Date	Total Indiv.	Total Captures (Prob. of capture)	Selected Model	Pop. Estimate (95 % C. I.)	MMDM	Density mice/ha	S.E.
E. Anacapa	IP (EA 1)	3/98	10	21 (.70)	M (o)	10 (8-12)	2.51	12	11.4
		11/99	65	141 (.71)	M (o)	66 (63-69)	1.65	107	9.2
		3/00	16	31	M (t)	16 (15-17)	1.76	27	9.5
		6/00 ^	43	82 (.6)		45 (40-50)		71	10.0
		7/00 ^	90	146 (.46)		107 (94-120)		137	27.7
		8/00 ^	112	200 (.54)		124 (114-134)		206	26.8
		9/00 ^	119	216 (.55)		130 (121-139)		209	22.2
		11/00 ^	130	239 (.56)		141 (132-150)		235	24.0
San Miguel	NI	4/93	46	112 (.81)	M (o)	46 (44-48)	1.61	99	5.4
		10/94	168	2 (.43)	M (b)	206 (174-238)	.86	339	87.0
		4/95	49	94 (.37)	M (b)	65 (53-113)	1.52	131	62.4
		10/95	167	254 (.40)	M (o)	214 (191-237)	1.02	311	65.2
		3/97	84	175 (.68)	M (o)	87 (84-91)	1.35	195	19.6
		7/97	201	349 (.36)	M (h)	315 (284-358)	1.34	311	70.3
		3/98	62	127 (.66)	M (o)	64 (60-68)	1.37	155	20.1
		10/98	255	327 (.24)	M (o)	454 (381-527)	1.88	981	230.7
		6/99	156	278 (.44)	M (h)	213 (191-235)	1.18	415	64.2
		4/00	52	94 (.55)	M (o)	57 (51-63)	1.63	87	19.7
		10/00	165	285	M (bh)	176 (164-188)	.87	210	59.3
		4/93	26	48 (.58)	M (o)	28 (24-32)	5.62	63	19.5
		2/95	35	65 (.58)	M (o)	37 (32-42)	1.04	84	19.8
San Miguel	AS	10/95	143	218 (.40)	M (o)	182 (161-203)	1.27	418	83.2
		10/96	127	199 (.42)	M (o)	157 (143-179)	1.10	380	58.1
		3/97	38	54 (.34)	M (o)	53 (44-75)	1.43	113	50.5
		7/97	145	252 (.37)	M (bh)	156 (145-167)	1.13	326	38.3
		10/97	111	210 (.59)	M (bh)	111 (111-111)	.95	278	31.1
		12/97	68	110 (.46)	M (o)	81 (70-92)	.88	160	30.1
		3/98	44	93 (.69)	M (o)	45 (42-48)	1.13	95	6.9

DEER MOUSE TREND REPORT

Island	Grid	Date	Total Indiv.	Total Captures (Prob. of capture)	Selected Model	Pop. Estimate (95 % C. I.)	MMDM	Density mice/ha	S.E.
San Miguel	AS	6/98	140	215 (.41)	M (o)	177 (157-197)	.9	436	70.9
		10/98	242	317 (.26)	M (o)	406 (344-468)	.71	682	174.1
		5/99	155	262	M (h)	220 (197-243)	1.09	543	74.8
		10/99	171	275 (.45)	M (h)	255 (229-282)	1.09	531	79.9
		4/00	19	41 (.72)	M (o)	19 (17-21)	2.31	19	5.8
		10/00	151	286	M (o)	162 (153-171)	1.14	290	28.7
San Miguel	WC	4/93	19	36 (.61)	M (o)	20 (17-23)	1.72	26	8.06
		10/95	139	179 (.24)	M (h)	243 (204-308)	.6	375	124.6
		10/96	100	124 (.21)	M (o)	196 (155-271)	.79	336	185.6
		3/97	15	23 (.43)	M (o)	18 (12-24)	1.20	28	27.2
		7/97	165	269 (.32)	M (th)	273 (227-354)	.99	367	55.8
		10/97	132	186 (.33)	M (o)	189 (159-219)	.9	230	70.8
		12/97	24	33 (.32)	M (o)	35 (21-49)	.29	84	69.6
		3/98	16	23 (.37)	M (o)	21 (12-30)	1.47	40	28.1
		6/98	113	193 (.50)	M (b)	158 (110-206)	.68	205	145.6
		10/98	211	240 (.13)	M (h)	388 (350-425)	.36	692	101.7
		5/99	135	196 (.47)	M (b)	158 (136-180)	.91	329	58.6
		11/99	186	288 (.41)	M (o)	233 (210-256)	.84	539	69.0
		4/00	14	26 (.60)	M (o)	14 (11-17)	2.38	35	8.0
San Miguel	DLB	8/96	131	241 (.31)	M (h)	154 (145-172)	1.74	187	30.0
		8/97	183	310 (.35)	M (o)	223 (204-242)	1.10	254	40.9
		8/98	272	394 (.25)	M (o)	399 (355-443)	1.21	576	109.5

(*) - 8 x grid

(^)- data collected by Island Conservation and Ecology Group (ICEG), Anacapa Island Restoration Project